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PROFILES OF PEATLANDS WITHIN LIMITS OF EXTINCT GLACIAL LAKES AGASSIZ AND WISCONSIN

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(WITH THREE FIGURES)

The present paper is a further attempt to show the connection between profile sections of peatlands and the environmental conditions which determined the formation of peat deposits in this country. The chief controlling field condition, which is here emphasized, is of exceptional importance in so far as it has a bearing on the selection and relative value of peatlands for different uses.

For Ohio peat deposits, a former paper (7) outlined the greater stratigraphic complexity of certain peatlands found within the older morainal belts. Although not all peat deposits necessarily date back to early postglacial times, the profile sections varied in more or less direct relation to the conditions which caused the successive positions of the receding ice sheet.

In a more recent article (11), it was shown that in the New England states the individual profiles of widely separated peat areas could be correlated. They confirmed the little that is known about the recessional moraines in that region. The study assigned to these deposits an approximate date, which, although not as yet expressed as so many years before the present, could nevertheless be referred to a certain time estimate in which the formation of the peatlands began in the respective localities. Among other things, the fact that

stratigraphic sections of different peatlands do not follow the usual order of the successional trend observed in the zonation of surface vegetation, was cited as an indication of changes in the external conditions, chiefly the amount of water from precipitation, which attended the peat formation.

The additional material upon which the present paper is based, was collected several years ago in Minnesota (1919) and Wisconsin (1922).[1] The purpose of the field study was to learn how far and in what ways the order of peat layers in western states depends on differences in external conditions, and to check up correlations connected with records from flooded valleys, ponded lakes, and plains which resulted at the closing stage when the ice sheet withdrew in the western region of the Great Lakes. The conditions to which the glacial lakes Agassiz and Wisconsin owed their existence have received a large share of attention from geologists. It seemed desirable, therefore, to study briefly the pedomorphic structure of the peat deposits which overlie these extinct lake beds. In this connection an attempt was made to evaluate the several field conditions that are usually cited as controlling the formation of peatland.

In regard to the method of investigating peatland, it is important to emphasize that accurate field information depends largely on the botanical identification of the plant remains which form more or less distinct and separate layers of peat. DAVIS (**12**), HUELS (**14**), SOPER (**25, 26**), and others have mentioned the botanical character of peat as a means of studying and classifying respectively the Minnesota and Wisconsin peat resources. The connections, however, which SOPER and OSBON, and preceding them DAVIS supposed they had made between "turfy, fibrous, earthy, and pitchy peat" and the botanical composition of the several layers of plant remains cannot be right, because these descriptions are not characteristic. Moreover, they have not made the botanical constituents a basis either for establishing stratigraphic differences, for identifying and coordinating layers of peat in widely separated localities of a region, or for working out the records made by the migrating vegetation,

[1] Valuable cooperation and aid for visiting the localities have been received from R. S. WHITSON, O. R. ZEASMAN, and W. J. GEIB of the Wisconsin College of Agriculture, and from J. J. ROSE, and W. M. EVERTS, state drainage engineer in Minnesota. It is a great pleasure to express appreciation for this assistance.

and the history of past environmental factors. On the contrary, these writers and others have attached much scientific interest to the general laws relating to the sequence of surface vegetation on peat deposits. The ecology of peatlands, indeed, may be regarded as a subject of its own for a correct understanding of the relationship of plants to their environment and the conditions under which vegetation of different types can grow. But peat deposits have been subject also to changes, in degree depending upon the time element involved in their formation. The limitations of a system of classifying peatland based on the sequence of surface vegetation have been briefly considered in a previous paper (**6**).

A detailed account of the writer's field practice has been given elsewhere (**9**), together with photographic illustrations of different kinds of peat and the chemical analyses of certain of their organic substances (**10**). Charts of profile sections, to show the widely varying differences in peatland, were included in several of the papers. In these pedomorphic studies of correlating series of layers of peat at one locality with the layers of plant remains in another locality, the starting point has been made for new peat investigations, which will be apparent to any one examining the data. Clearer conceptions are now possible concerning type profiles and the physical and chemical composition of the different layers of peat. A better understanding may be obtained as to the nature of the transformation of plant remains from peat to muck and humus, and the products brought about by the activity of microorganisms. Profile records will bring out the conditions under which drainage, cultivation, fertilizing, and systems of farming should take place. Agricultural as well as industrial problems in peatland utilization will see their practical solution when a thorough line of observation is made in each important peat area. Through the measurement and coordination of profile sections, the experimental and economic correspondences can be finally made for regional groups of peatland selected on a stratigraphic basis. A chief disadvantage has been the lack of adequate field data. It is hoped that other investigators may become interested, so as to secure and study in detail a greater number of profile sections, particularly in areas which are physiographically uniform.

I. Profiles of peat deposits in area of glacial Lake Agassiz

Glacial Lake Agassiz covered much of the Red River basin and the northwestern portion of Minnesota (fig. 1). It extended westward into the prairie region of North Dakota, and northward far into Manitoba and Ontario, Canada. UPHAM's monograph (27) contains many important data on this former lake. Nearly its entire

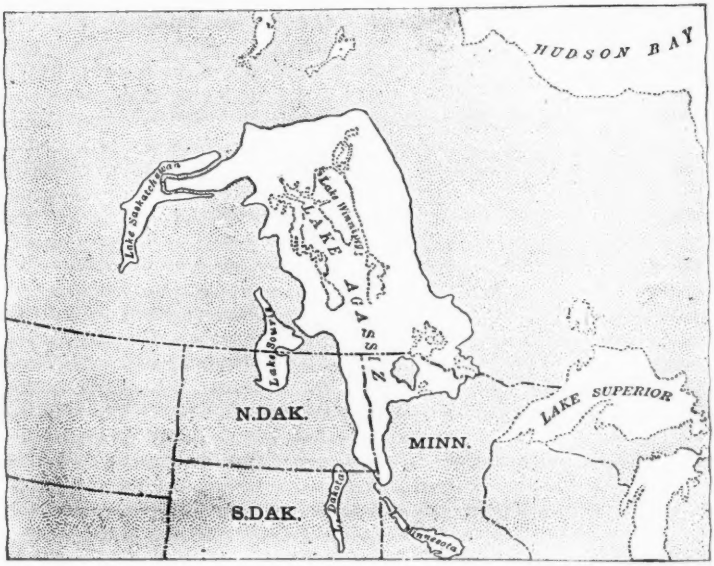

FIG. 1.—Map of extinct Lake Agassiz, and other glacial lakes (UPHAM, U.S. Geol. Survey).

bed rests upon calcareous gray drift, which had been carried in previously by the Keewatin ice sheet.

The waters forming glacial Lake Agassiz were held back on the north in central Canada by glaciers, and for a long time they were ponded in front of the ice sheet. Preceding the development of this ancient lake there was a temporary older body of water. The ice that covered Ohio and the southeastern portion of this country had melted, while in the northwestern states glacial conditions appear to have been stationary through a long period. With the melt-

ing back of the northern ice border, however, the pre-Agassiz lake grew from south to north as the ice sheet receded. The highest stage of the waters in this largest of the many Pleistocene lakes was probably 500 feet above the present surface of Lake Superior (602 feet). In much of this area the waters were relatively shallow, and hence there were several islands in the lake. The level of the waters was lowered from time to time, forming beaches of sand and gravel along its shores. Several large deltas were formed contemporaneously with the higher shore lines, and for some time the lake probably received modified drift brought by streams from the receding glaciers. Gradually the lake was drained to the south through the Minnesota River (glacial river Warren at that time), partly by the cutting down of the outlet and partly by an uplift of this region.

The shores of Lake Agassiz generally stand 5–10 feet, and occasionally 15–20 feet above the lake washed till of the clayey and limey plains. Later, it seems, the lake area was again encroached upon by the ice sheet, since the shore lines are obliterated in places, except along the eastern side. Finally there was a change of outlet from the southern to the northern end. The waters escaped eastward into the Lake Huron basin, and later to the much enlarged Gulf of St. Lawrence. With the uncovering of Hudson Bay, the lake receded to its present position in Manitoba, where Lake Winnipeg is one of the remnants.

With the recession of the lake waters from the southern borders in Minnesota, large areas of land were uncovered. The southern and eastern borders of the lake were the first to become dry, and to be converted into marshes and forests by the incoming vegetation. Gradually these and the intervening isolated ponds and small lakes became the site of the extensive, flat peatland of today. UPHAM estimates that the recession of the ice sheet causing Lake Agassiz may have been from seven to ten thousand years ago, and that the duration of this great lake was probably not more than one thousand years. On the basis of this surprisingly short estimate for the duration of Lake Agassiz, therefore, the formation and accumulation of layers of peat have occupied not more than six to eight thousand years. In the course of that time to the present, several layers of peat have been formed in this region. The levels of the changing

surface vegetation and of the fluctuating ground water table were slowly raised, and the inequalities of the underlying topography, as well as the variety of mineral soils, disappeared under one of the largest peatland areas in Minnesota. To the pioneer settlers, nearly the entire portion of extinct Lake Agassiz in northern Minnesota was an unbroken expanse of "muskeg" swamp, in part timbered with spruce and tamarack, in part with open heath bogs and sedge marshes.

In the following paragraphs a description is given of some of the profile sections of the great muskegs which now cover a considerable portion of the ancient lake bed in Beltrami, Koochiching, and Roseau counties. The location and acreage of this peatland area are shown on LEVERETT's map of the surface formations (**15, 16**), and on the topographic and drainage map which accompanies House Document 27 of the Sixty-First United States Congress, first session. More recently the engineers in charge of state drainage projects have surveyed and sounded the depth of much of this peat area. Part of their data and maps have been included in SOPER's report on the peat deposits of Minnesota (**25**). Of the writer's data and field-work, only as much is given here as is necessary to show the connections among peat profiles from widely separated localities of the same lake bed.

1. SOUNDINGS IN T. *153* N., R. *26* W., S. *16*, ABOUT 50 FEET WEST OF THE PUBLIC ROAD.—The vegetation consists of a good growth of tamarack, cedar, and a few spruce, with heath shrubs such as *Ledum* in sphagnum mosses. Burned and cleared portions show *Potentilla fruticosa*. In the open state ditch nearby a horizon of lime accumulation is beginning to appear; it is readily recognizable by the lighter color and the effervescence upon application of acid. At this locality the depth to the underlying calcareous sandy clay varies between 5 and 8 feet. The several layers of peat are easily observed for a distance of several miles. Their order and thickness in the profile section of this vicinity are as follows, enumerated from the top downward.

Sphagnum peat: 6–8 inches; fibrous, relatively dry and light brown in color.

Woody peat: 1 foot in average thickness; dark brown, rather compact,

granular, with roots and stumps of conifers and woody fragments of various sizes; this grades into

Sedge peat: 3.5 feet; brown, finely fibrous, partly disintegrated, in places somewhat coarse and matted; sandy at lower level, with roots in gray sandy to gravelly clay.

2. TEST-BORINGS IN T. 154 N., R. 25 W., S. 21, ABOUT 200 FEET EAST OF MINNESOTA AND INTERNATIONAL RAILROAD.—This is the continuation of the tamarack-spruce-cedar muskeg already described. The layers in the profile section have the following sequence and thickness:

Sphagnum peat: 7–9 inches; light grayish brown, largely fibrous.

Woody peat: 12–14 inches; brown to dark reddish brown; consists largely of the woody fragments and granular remains of coniferous trees, with cones and needles; grading into

Sedge peat: 4–5 feet; brown, largely fibrous.

Woody peat: 1.5–2 feet; dark to very dark brown, in part poorly decomposed showing stumps and woody fragments of conifers with fibrous débris from roots; the underlying mineral is brownish gray, clayey sand over a bluish gray clay.

This profile section shows very good agreement with different test-borings in such portions of the same muskeg as are situated near Nakoda, Little Fork, and Wisner.

3. CONTINUATION OF MUSKEG SWAMP; SOUNDINGS IN T. 154 N., AND R. 25 W., SOUTHWEST OF BIG FALLS, MINNESOTA.—The test-borings show essentially the same profile, but the thickness of the layer of sedge peat is greater and includes a pocket of standing water between an upper and lower mat of sedge peat. The surface vegetation consists in places of scrub tamarack and spruce, but varies within relatively short distances. The depth of peat accumulation, however, bears no relationship either to the size or to the abundance of the conifers present. This supposition is strongly supported by the photographs which accompany SOPER's report (**25**). They show that in some of the largest and deepest peat areas tamarack and spruce are present in about equal numbers, without any tendency toward segregation or dwarfing. It must be assumed that some other factor or factors are decisive in determining the quality of timber produced. Field observations show that the volume of wood produced varies periodically. The pathologic condition which

lowers the quality and height of the timber appears to result from a reducing action and a slow rate of decomposition of the more resistant sedge or reed peat in the rooting horizon utilized by the forest trees. A slow rate of tree growth is to be expected when the ratio between the carbon and nitrogen content is in an unfavorable condition for decomposition, or when the water content is too high for any period of time, irrespective of the degree of decomposition and the type of the peat material which is occupied by the roots of the trees (10). The evidence from buried forests in peatland profiles is of a similar nature over a wide range of the country.

4. SOUNDINGS IN T. 154 N., R. 26 W., S. 11.—This is a part of the great muskeg swamp with spruce and tamarack covering several hundred square miles in Beltrami and Koochiching counties. Test-holes along a newly constructed road and observations in an open ditch show the order and thickness of layers as follows:

Sphagnum peat: 9–10 inches; gray brown, fibrous, moist.

Woody peat: 1 foot average thickness; chiefly the remains of a spruce and tamarack forest with charred woody fragments at lower level; this grades into

Sedge peat: 6–8 inches; brown, firm, partly fibrous.

Hypnum peat: 5–7 inches; yellow brown, poorly decomposed, with an admixture of fibrous material from sedges at upper level; fairly compact.

Woody peat: 1.5–2 feet; dark brown to very dark reddish brown, derived largely from tamarack and spruce; contains material from ferns, cones, and needles; layer rests on a brownish sandy clay which grades into light colored gray, sandy clay.

SOPER does not give profile sections in his bulletin on the peat deposits of Minnesota; consequently, the actual sequence and thickness of the individual layers of peat have not been worked out by him. So far as there is material for identification, however, SOPER'S description of the peatland in Beltrami and Koochiching counties shows certain agreements with the botanical characterization of the layers of peat just enumerated, and the correspondences between the different peat profiles are rather good. The agreement is quite striking regarding the basal layer of woody material which SOPER has recorded between points at distances of many miles. Accordingly, this shows a very wide spread of an ancient forest, with spruce and tamarack as its most typical constituent. This forest appears to have taken possession of the lake bed wherever local conditions

were not extreme. Climatologically this area must have been relatively uniform, for the forest vegetation undoubtedly indicates that the ground water table was low. The trees were growing under very favorable conditions for a considerable period of time, since the layer of woody peat is thick at all localities measured. The ice front must have been fairly distant.

Obstructions in drainage and a rise in water level evidently played a prominent rôle in the formation of the succeeding layers of *Hypnum* and sedge peat. These layers indicate rather strong disturbances. The presence of *Hypnum* mosses as a layer overlying woody peat is difficult to understand, and the circumstances under which the organic material was deposited are not clear. In SOPER'S account this section of the profile series cannot be identified, since his descriptions are not characteristic for corresponding situations. In this vicinity the *Hypnum* layer is relatively thin, and appears to have accumulated in shallow water. Farther north, near Algoma in Roseau County, the layer is present in considerable thickness, and contains an admixture of somewhat coarse plant remains from species of *Equisetum* and sedges. It is not unlikely that *Hypnum* peat represents conditions of growth in cold glacial waters which came from an ice sheet readvancing to a point some distance north of this locality. When the ice again withdrew, and outlets for glacial waters were uncovered, the stages to sedge peat and finally to the uppermost level of woody forest peat may correspond with the changes in water level and the shifting of the climatic conditions accompanying the ice recession into Canada.

The profiles enumerated correspond with those which were outlined for peat deposits at Chassel, Michigan, occupying the marginal portions of the glacial Lake Algonquin (**8**).

II. Profiles of peat deposits within area of glacial Lake Wisconsin

This former body of water was in the Driftless Area between the Wisconsin and Black Rivers. It probably covered at least 1825 square miles. The extent and form of glacial Lake Wisconsin and the positions of some of its glacial streams are shown in fig. 2, from MARTIN (**18**). The lake was held in by the margin of the ice sheet

to the east of the Driftless Area. The waters rose to a height of 960–1000 feet above sea level, being about 70–150 feet deep. Clay, sand, and erratic bowlders from floating icebergs constitute the chief deposits of this lake; they form a relatively impervious bottom over the porous Cambrian sandstone underlying this area.

Glacial Lake Wisconsin is believed to have been relatively short lived; it produced few well defined shore lines. At present these shore lines are not horizontal, but tilted by an uplift. They rise toward the north, and increase in altitude from 960 feet near Baraboo and Kilbourn to almost 1000 feet to the north about 55 miles, near City Point. When the ice had melted back from the valleys near Baraboo, the waters of glacial Lake Wisconsin cut through the terminal moraines to the southeast until the lake was drained out. The waters may have escaped to the west through the Black River outlet, however, since deposits of this lake extend out into the plain west of the Black River divide. It is not yet known at what time glacial Lake Wisconsin ceased to exist. It appears to have been coexistent with glacial Lake Agassiz.

After the lake was drained, rather large streams seem to have been at work, spreading outwash gravels and other material over some areas within the lake basin. Subsequently the lake deposits were subjected to wind action. In many places dunes and loess-like material were formed. In the northern and northwestern part of the basin the lake deposit is white quartz sand, owing to the large area of crystalline rocks in the north. This lake bottom sand, underlain in turn by impervious clay, is now the mineral subsoil of large areas of peat, and may be well seen along the extensive drainage ditches of Wood, Juneau, and Jackson counties. The finer detritus was carried farther off shore, and spread over the lake bottom as calcareous clay. In the southern part of the lake basin the soils are reddish silts and sandy clays.

Today glacial Lake Wisconsin represents the largest peatland area in the state of Wisconsin. It is known generally as the Great Swamp of Central Wisconsin (fig. 3). Maps showing acreage and location are given by MARTIN (**18**). Its surface vegetation included numerous open sedge and reed marshes with no timber, as well as

areas forested with tamarack, spruce, and occasionally white pine. The accumulation of peat varies in depth, and covers a variety of topographic features and mineral soils over an area of nearly 300,000 acres. At present parts of this extensive deposit are used

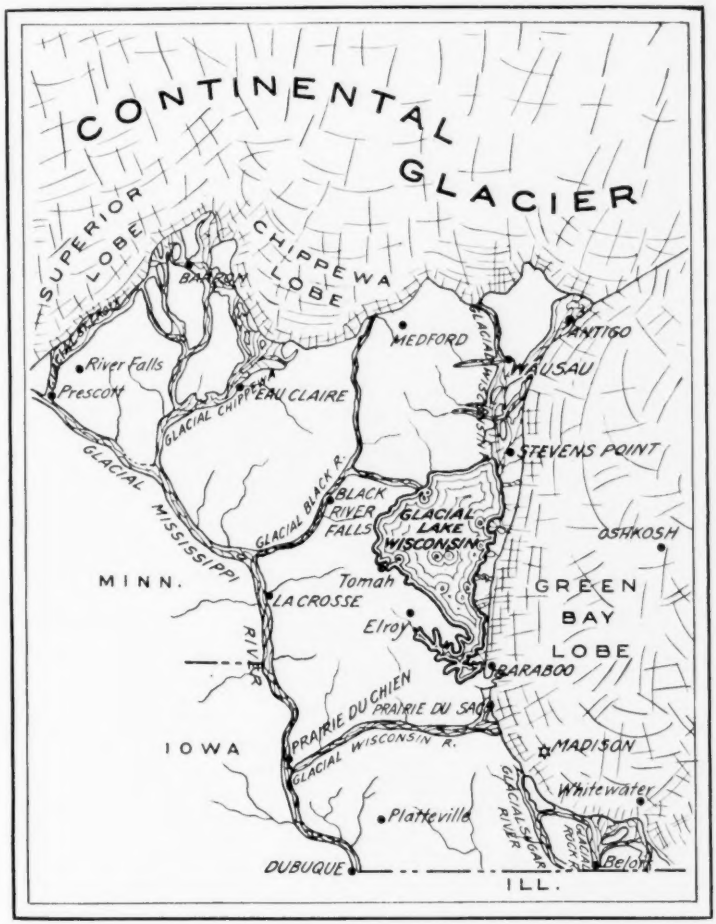

FIG. 2.—Driftless area at Wisconsin stage of glaciation (MARTIN, Wis. Geol. & Nat. Hist. Survey).

for cranberry fields; in others sphagnum moss is gathered and shipped to florists. Relatively little of this area appears to be under cultivation in general farm crops.

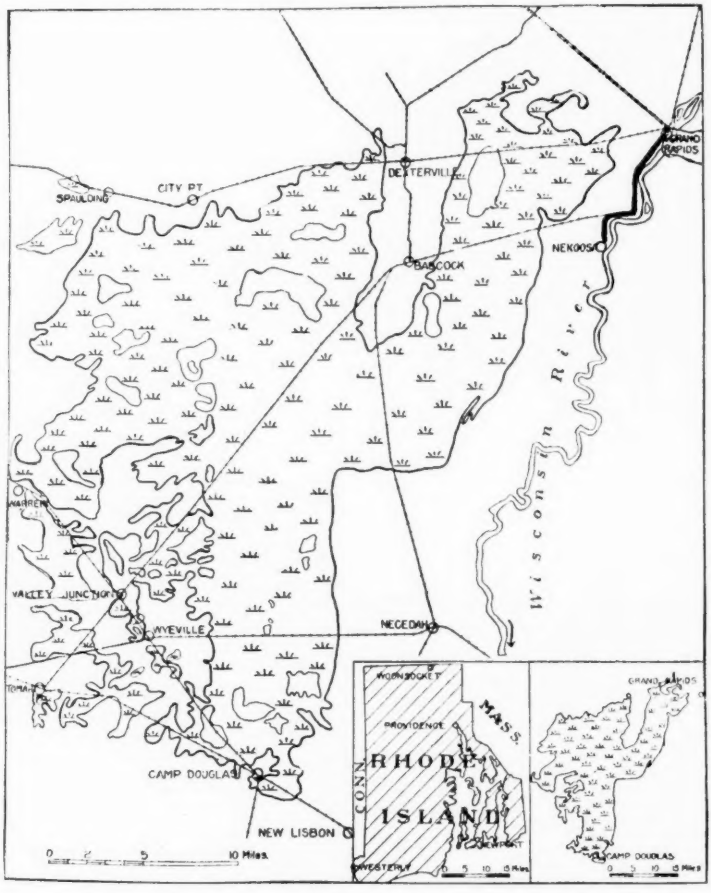

FIG. 3.—Great swamp of central Wisconsin (MARTIN, Wis. Geol. & Nat. Hist. Survey).

A few of the individual peatland profiles will be discussed, with comments on the cross-sections which occur in the same areas at widely separated localities. As in the profiles from the region of gla-

cial Lake Agassiz, all minor variations in plant remains and disturbances due to quite local conditions have been discarded, or merged into the chief layers which showed characteristic botanical features and average conditions.

1. WARRENS, WISCONSIN.—The profile section of this locality is northeast of Warrens in T. 20 N., R. 1 E., in the southeast quarter of Section 28. The area is under cultivation, and has been burned over repeatedly. It is reported to have had in places a surface vegetation which consisted of tamarack with heath shrubs, and a ground cover of sphagnum mosses and other plants characteristic of a northern conifer swamp. The profile, as shown by test-borings, which may also be observed in the large open ditch draining this part of the peatland area, is as follows:

Sphagnum peat: burned off.

Woody peat: largely burned off; woody fragments from stumps and roots at intervals.

Sedge peat: 5 feet in thickness; brown to dark brown in color, fibrous, somewhat matted, and in part disintegrated.

Woody peat: 1 foot in average thickness; dark to very dark brown, largely well decomposed, with roots and stumps of tamarack and spruce; underlying mineral soil is gray siliceous sand.

In striking agreement with this profile are the cross-sections from the "Leola Marsh" near Plainville, and from the "Buena Vista Marsh" near Coddington. The latter contains a thin bed of gray loess-like silt and a layer of *Hypnum* peat below the basal forest peat. The profiles resemble closely the cross-section from peatland at Lake Forest near Madison, and at Cottage Grove, Wisconsin. Considering the different position of the localities in relation to the glacial lake bed, the correspondence of the profiles is good and their thicknesses agree well.

2. CITY POINT, WISCONSIN.—This peat area is an isolated portion of the Great Swamp of Central Wisconsin, and is located west of City Point in T. 22 N., R. 1 W., S. 26. The original vegetation included tamarack and spruce with heath shrubs. At points about 600 feet south of the public road and the Green Bay and Western Railway, test-holes show the following profile features:

Sphagnum peat: 8–10 inches; gray brown, fibrous.

Woody peat: 4–6 inches; dark reddish brown coarsely fragmented with

fibrous material from sedges into which coniferous trees and various shrubs spread their roots at different ranges of depth.

Sedge peat: 7–8 feet in thickness; brown to dark brown; varied in texture from finely fibrous to matted material, frequently with an admixture of coarse plant remains from reeds; at lower level the material is more or less disintegrated in place, with occasional root fibers in a brown colored sandy organic débris which grades into gray, compact siliceous sand.

3. Similar profiles to that found near City Point, Wisconsin, were observed in the continuation of this same great swamp between Tomah and Wyeville, in a white pine-tamarack swamp in T. 20 N., R. 1 E., S. 20., and at a locality in Wood County referred to as the Searles cranberry marsh. They show a rather good correspondence with one another. At the Searles locality the profile section was obtained in a large drainage ditch which was under construction at the time of visiting this vicinity. The thickness and botanical composition of this peatland area were exposed in the sides of the ditch for a considerable distance. The surface vegetation consisted of tamarack, spruce, heath shrubs, and a varying ground cover, chiefly of sphagnum mosses. The underlying mineral soil is sand.

The report of HUELS (14) on the peat resources of Wisconsin does not contain information relative to the counties within the limits of glacial Lake Wisconsin. HUELS includes from the survey of 1903 the description of a deposit three miles northwest of Babcock in Wood County. This record seems to indicate a profile similar to those just mentioned.

III. Relative importance of conditions which controlled formation of peatland in glacial lakes Agassiz and Wisconsin

The question now arises as to the basic conditions which determined the formation of peatland after the draining of the glacial waters. This problem is particularly important, whether relating to forest trees, soil microorganisms, or farm crops.

The processes of peat formation are probably essentially the same at the present moment as in the period immediately following the recession of the ice sheet, but not so the general external conditions under which the different layers of peat originated. It is generally

stated that the most important factors in the development of peat deposits are topography, soils, geology, and climate. These conditions are not infrequently cited as determining the main possibilities, as well as the main limitations of peatland agriculture. It is not purposed to enter into an extended discussion of the physical basis of peatland formation in the United States. The object here is to discuss briefly the larger environmental relations recorded in the profile of the peatlands within the ancient lake beds, with such references to the literature as point the direction of more special subjects of investigation.

1. The influence of the topography of any underlying land surface is usually cited as the most important external condition in the origin of peat deposits, as well as in their distribution and classification. This attitude is frequently expressed in the statement that, no matter how favorable the climate or the soils may be, peat cannot accumulate unless the topography is such that lakes, ponds, or other poorly drained depressions prevail.

It is customary to speak of any large portion of land as a topographic unit when it represents broad similarities among certain features, such as have been expressed, for example, for the glacial lakes Agassiz and Wisconsin. Nevertheless, the idea of a topographic unit cannot be applied to the beds of the two extinct lakes in an absolutely rigid manner. The description of these large basins shows that marked dissimilarities prevailed in geologic structure, physiographic processes, and time of development in the postglacial cycle. Similarly, topographic features, such as slopes, undulating surfaces, barriers, and depressions due to old stream channels and erosion varied from point to point in the two lake beds; yet examination of the peat profile sections shows conclusively that nearly everywhere plant remains were deposited and transformed into layers of peat in a relatively dry bottom of a flat, but not level lake bed. The great horizontal extent of the basal forest peat, the high degree of parallelism in the profile sections from widely separated localities, and the recognition that these extensive peat areas originated after the draining of the glacial waters, all these facts indicate that peat deposits are far from showing an exclusive relation to topographic conditions. The peat areas under discussion were not con-

fined to any one feature of topography, and they are not the effect of varying subsidence. To what extent the original drainage channels have been cut deeper as the land rose cannot be said; at present the peatlands do not disclose the character of the underlying land surface. The topographic variations have all been smoothed over and covered with several distinct layers of peat differing in origin and composition. Neither the horizontal areal extent, nor the vertical level which marks the present stratigraphic limit of peatland formation seems to have any direct bearing on topographic features.

2. The effect of underlying mineral soils upon the formation and distribution of peat deposits has been the source of much controversy in the literature which deals with the dependence of peatland upon environmental conditions. SENDTNER (**22**) and LORENZ (**17**) were probably among the first to state that the distribution of vegetation on peat deposits depends upon the chemical composition of the underlying soil and soil waters. The absence of lime was regarded as the characteristic feature, but not acidity. WEBER (**29**) assumed that lake basins are successively modified in content of mineral matter, such as lime, when the depressions become filled with peat. The term eutrophic is used by him for peat materials formed in water rich in mineral nutrients; oligotrophic for types with water poor in saline food constituents; while mesotrophic is applied to peat layers in the intermediate stage. ZAILER and WILK (**31**), BERSCH (**4**), BIRK (**5**), MINSSEN (**20**), and WARÉN (**28**) give a large number of chemical analyses. Their results show the changes of the mineral matter in different kinds of plants which form peat, and in the corresponding peat material derived from them. These investigators found that the ash content does not increase with the depth of a deposit, but varies with the character of the profile section and with the contamination by extraneous silt, lime, or ferruginous compounds. It is important to note at this point that certain layers of peat, when in contact with water, lose practically all the alkaline salts and phosphates entering into the composition of the vegetation from which they were derived (**10**). The elimination of oxygen from the organic débris also is proportionally much greater than that of the other elements, as the water table becomes elevated with the formation of peat. The peat materials become increasingly unsatu-

rated (3), that is, they show reduction action and are relatively more acid, but this acidity follows the accumulation of peat; it does not cause the occurrence and distribution of peatlands. The acid reaction of the surface horizon of a peat soil does not necessarily indicate the varying intensities of the reaction of the underlying layers of peat or of the mineral subsoil. Moreover, PAUL (21), SKENE (24), MEVIUS (19), and others have not been able to find any very marked correlation between the acidity of a peat soil and its cover of vegetation. It thus appears unlikely that acidity alone is producing the observed differences in the stratification of peatland or in their surface vegetation. It must be realized also that the microorganic population of a peat layer is sensitive to the reducing action of the medium, and that fluctuations in the oxygen content will presumably produce a marked effect, both on the species and numbers of such soil microorganisms, and on the rate of the decomposition of peat.

From an inspection of the geologic maps of Minnesota and Wisconsin, it will be seen that peat areas in these states are not confined to any one geologic formation. Furthermore, the recent mapping of the boundaries of the drift sheets by LEVERETT (15, 16), and of the diversity of soils by the United States Bureau of Soils have made available many data bearing upon this problem. These facts show that the peat area, found in the bed of former Lake Agassiz, rests in large part upon calcareous gray drift, while the Lake Wisconsin peatland, in the Driftless Area of that state, is not confined to any one drift cover, but occurs on a variety of water sorted and wind drifted glacial material, in some localities calcareous, in others lacking in lime. These instances suggest that, relative to the presence or absence of lime in the rocks composing the drift and in the chemical composition of the underlying mineral soils, differences of that kind do not determine the extent, thickness, or parallelism in the layering of the widely separated peatlands. The effects of differences in quantity and quality of salt content, especially in lime, become observable as a rule after drainage, and more particularly under cropping systems which favor evaporation of ground waters at the surface. WHITSON (30) found that marshes which are acid become well supplied with lime by the waters percolating through

the soils and rocks of the surrounding region. ALWAY (1) states that burning surface layers of peat in some cases may produce an alkali soil.

It would lie outside the limits of this paper to provide further data necessary to establish the view that no direct connection appears to exist between the development of peat deposits, both in quality and thickness of different layers, and a high or low lime content of the glacial lake beds and their drainage waters. The inauguration of peat formation, as well as the sequence of peat layers, obviously must be regarded as being largely independent of the chemical composition of the mineral soils. Distinctions on the basis of acidity or lime content appear to be inadequate for purposes of classifying peat deposits. The evidence at hand does not indicate that these are the controlling influences in the origin and stratigraphic similarity between the peatlands of the two glacial lake beds.

3. Climate, more particularly the climate of the past as a determining factor in the origin and structural features of peatlands, has only recently received the impartial consideration which it deserves. In Europe the development of this viewpoint by BLYTT (2), SERNANDER (23), and others has again received strong support by the more recent work of GAMS (13), RUDOLPH and FIABAS, and others.

The ice retreat in this country and in Europe does not appear to have been very different. The halt and readvance of the ice edge reflect climatic fluctuations, and when the morainal belts of the respective countries are properly matched, they show agreements in several respects (8).

The recession of the ice sheet marks the beginning of many peatlands in the glaciated regions of this country. In the western states the ice edge stood practically still for a considerable period of time, while it receded in the southeastern part of the country. The explanation is that probably in Minnesota and Wisconsin the summers were cold, the air was still very foggy, and the temperature low and constant in a belt off the ice front, while in the Ohio-Indiana region the sky was clear, and warm days were frequent. At that time, as today, the most important among the elements of climate in relation to types of vegetation, and to the quantity and character of peat

derived from them, must have been moisture from precipitation, and temperature. In the course of time the warmer zone shifted northward and the ice front retreated. As the surface waters of glacial lakes Agassiz and Wisconsin became reduced by run off and evaporation, the extent of peat accumulation over the uncovered land varied from time to time. The structural differences, as shown by the evidence presented in the profile sections, undoubtedly correspond in a general way with climatic changes. Precipitation may have played the leading part, since as a rule the amount of water shows greater effects upon peat formation in a topographically similar area, than does temperature. The conditions at the ice front had become milder and more stable when the basal conifer forest, essentially similar to the present vegetation, invaded the dry portion of the lake beds. After a time interval of considerable length, the physical conditions under which the forest trees grew ceased to exist. Changes in drainage, water supply, and atmospheric relations (again cooler and probably more humid) resulted in a new set of environmental surroundings, to which sedges and reed marshes, and in places *Hypnum* mosses, were better fitted to dominate. The presence of *Hypnum* peat seems to record a temporary readvance of the ice. The layer of buried forest is not always sharply differentiated from the fibrous peat material which formed above it. The vertical limits at times are difficult to distinguish; they evidently correspond to a gradual change in physical conditions.

Upon the surface of the sedge formed peat layer, a conifer forest once more made its appearance and began to spread over the open marshes. Essentially more favorable climatic conditions, warmer and drier, and related soil conditions prevailed, under which the forest vegetation of the conifer belt could grow and extend itself over peatlands. Reforestation and the accumulation of woody peat were again the characteristic features when the first settlers appeared. These conditions are in sharp contrast with the moisture relations which favored the long continued dominance of marsh vegetation. They must have been notably affected by lighter, more moderate rainfall; better aeration and decomposition must have taken place in the surface horizon of the peat soil.

Summary

In conclusion, it should be stated that it is the climatic aspect of peat profiles which needs to be emphasized also in matters relating to the agricultural uses of these lake-bed peatlands. From the foregoing considerations it is evident that the present native surface vegetation is no indicator, either of the depth of peat accumulation, the sequence of layers, the character of the mineral subsoils, or the production possibilities for different systems of cropping. The profile sections indicate, furthermore, that production in these peat areas may depend chiefly on the quantity of water available. During the period before settlement, the arable land resources of the states had become filled with ground water from a long accumulation of rainfall and thaw waters. Since the settlement of the states, the ground water level has been steadily sinking. A serious situation may arise, therefore, in periods of drought, and settlers in that region may not be able to endure the years of adversity, if an extensive system of drainage is adopted without reference to the stratigraphic features of the peatlands. The provision of an adequate water supply and the control of water levels is essential if the agriculture of the region is to be permanent and satisfactory. The lack of a commensurate water supply may operate entirely against increasing production by intensive methods of farming. Such portions of the forested peatland area which contain deep, water logged depressions are important water storage basins. They would help to regulate and maintain a favorable ground water table. It seems far more profitable, therefore, to select such localities, and not to drain them, but to keep them as part of a state reserve of reforestation.

U.S. DEPARTMENT OF AGRICULTURE
WASHINGTON, D.C.

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NEW OR OTHERWISE NOTEWORTHY COMPOSITAE. II

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 341

EARL EDWARD SHERFF

(WITH PLATES XIX–XXII)

In a former article[1] were discussed various specimens of *Bidens*, *Coreopsis*, *Cosmos*, *Isostigma*, etc., which had been found either to represent new species or to be otherwise important. Most of the specimens there cited were in the Herbarium of the Botanical Garden of Berlin. In the summer of 1924 I was privileged to visit Europe and examine many specimens of these genera. Some of the noteworthy specimens of *Isostigma* and many of those of *Bidens* will receive separate treatment in two forthcoming articles. Much of the other material, found chiefly in Berlin, Geneva, Paris, London, and Kew, will be considered here.

Coreopsis senaria Blake & Sherff, sp. nov.—Frutex; ramuli angulati lineatim hispiduli, internodiis brevibus; folia opposita brevia usque ad petiolos brevissimos connatos palmatim 3-partita, segmentis anguste lineari-oblanceolatis ca. 7 mm. longis 0.8 mm. latis; capitula solitaria in pedunculis brevissimis hirtellis insidentia; phyllaria interiora 8–9 exterioribus ca. 18 biseriatis lanceolatis ciliatis dimidio longiora; achaenia piloso-ciliata; aristae sursum ciliatae.

Shrub; branches 6-angled, rather slender, covered below with the persistent leaf bases, hispidulous in 2 lines; internodes 5–10 mm. long or less; leaves opposite, with axillary fascicles; petioles 1–1.5 mm. long, connate throughout their length, glabrous; blades palmately 3-parted to base, the lobes narrowly linear-oblanceolate, 6–8 mm. long, 0.6–0.9 mm. wide, with acute, callous tips, entire, fleshy, glabrous, dark green, 1-nerved, veinless; peduncles solitary at tips of branches and the few branchlets, monocephalous, hirtellous, few-bracted, 1 cm. long or less; heads about 2 cm. wide; disk

[1] BOT. GAZ. **76**:78. 1923.

about 7 mm. high, 9 mm. thick; involucre 7.5 mm. high, the outer phyllaries about 18, distinctly 2-seriate, subequal, herbaceous, lanceolate or linear-lanceolate, obtuse to acutish, often apiculate, 3-nerved, ciliate about to middle, glabrous dorsally, 4–5 mm. long, 1 mm. wide, the inner 8–9, membranous, oblong, obtuse, brown with narrow yellow margin, ciliolate, otherwise glabrous, 2.5 mm. wide; rays (probably 8) golden yellow, neutral, the tube glandular-puberulous above, 1.8 mm. long, the lamina oblong-oval, about 6 mm. long, 3 mm. wide, 11-nerved; disk corollas yellow throughout, sparsely puberulous toward apex of tube, 3.9 mm. long (tube 1.3 mm., throat slenderly campanulate-funnelform, 1.8 mm., teeth ovate, 0.8 mm.); pales lanceolate, 4 mm. long, acuminate, ciliate, pilose along midline, 5-nerved; disk achenes (very immature) obovate-oblong, pilose-ciliate on margin and at apex, glabrous on outer face, somewhat pilose on inner; awns 2, lanceolate, upwardly pilose-ciliate, 2.2 mm. long.

PERU: On punas, collected on an excursion from Pacasmayo to Moyobamba, April to June, 1875, *A. Stübel* 35 p.p. (type in Herb. Berl.; photog. and fragm. in U.S. Nat. Herb. no. 1,194,718).

Nearest *Coreopsis foliosa* Gray, but very distinct from that and from all other South American species in its leaves, which are palmately 3-parted down to the apex of the petiolar sheath. The species is unique also in its numerous and narrow outer phyllaries.

This and the next five species, all from South America, were submitted to SIDNEY F. BLAKE, Associate Botanist of the Bureau of Plant Industry, Washington, D.C., for examination. He had already made a critical study of the South American species of *Coreopsis* and was quick to recognize these as new species.

Coreopsis parviceps Blake & Sherff, sp. nov.—Frutex glaberrimus; rami angulati; folia opposita petiolata, inferiora 2–4-partita lobis linearibus vel lineari-ellipticis, superiora integerrima lineari-elliptica; capitula parva solitaria breviter pedunculata; involucri 6 mm. alti phyllaria interiora 8 oblonga glabra exterioribus 6 linearibus glabris duplo longiora; achaenia piloso-ciliata; corollae disci aristis ciliatis dimidio longiores.

Trichotomous shrub, essentially glabrous throughout; stem terete, striatulate, gray-barked; branches and branchlets slender, striate-angled, brownish; internodes 1.5–4 cm. long; petioles slender, 3–8 mm. long, connate into short cups, these slightly ciliolate in the

sinuses; lower blades deltoid in outline, about 2.2 cm. long, 2.8 cm. wide or less, palmately 2–3-parted or sometimes with 2-parted terminal lobe, thickish, glabrous, dark green on both sides, subpunctic-ulate, the lobes linear or linear-elliptic, 9–16 mm. long, 1.8–3 mm. wide, acute, translucently feather-veined; upper blades entire or sometimes 3-lobed, linear-elliptic, 8–19 mm. long, 1.5–3 mm. wide; peduncles solitary at tips of branches and branchlets, monocephalous, slender, glabrous, about 2.7 cm. long; heads 1.8 cm. wide; disk 6 mm. high and thick; involucre 6 mm. high, the outer phyllaries 6, thick-herbaceous, linear-oblong, 3 mm. long, 0.8 mm. wide, obtuse, glabrous, the inner 8, membranous, elliptic-oblong, 6 mm. long, 2.5 mm. wide, obtuse, glabrous, erose at apex, yellow with many brown nerves; rays 8, neutral, golden yellow, the tube pilosulous, 1.5 mm. long, the lamina oval, 7.5 mm. long, 4 mm. wide, 12-nerved, sub-entire; disk corollas rather few, golden yellow, sparsely puberulous at apex of tube, 3.5 mm. long (tube 1 mm., throat campanulate-funnelform, 1.6 mm., teeth ovate, 0.9 mm.); pales oblong-obovate, 3.5 mm. long, truncate or emarginate and somewhat spinulose-ciliate at apex, sparsely pubescent dorsally, about 5-nerved; ray achenes (inane) oblong, pilose-ciliate, sparsely pilose inside on midline; disk achenes (very immature) oblong, pilose-ciliate, ciliate at apex, pilose inside along midline; awns 2, lanceolate, upwardly pilose-ciliate, 2 mm. long; style tips deltoid-triangular, acuminate, hispidulous.

PERU: Tambillo, August 19, 1878, *de Jelski* 765 (types in Herb. Berl.; photog. and fragm. in U.S. Nat. Herb., no. 1,194,717).

Nearest *Coreopsis foliosa* Gray and *C. glaucodes* Blake & Sherff. The former has densely pilosulous and densely leafy branches, 3-parted leaves with lobes 1.2–2 mm. wide (the terminal one 3-partite), and oblong, rather densely pilosulous outer phyllaries. The latter is glaucous, with less deeply cut leaves and very narrow outer phyllaries.

Coreopsis glaucodes Blake & Sherff, sp. nov.—Frutex glaberrimus, partibus novellis glaucescentibus; folia opposita ambitu saepius cuneata vel rhombica ad medium vel ultra trilobata, lobis integris vel terminali tridentato oblanceolatis vel lanceolatis acutis; capitula parva 1–4 ad apices ramorum; involucri 4–6 mm. alti phyllaria interiora 8 exterioribus 8 anguste triangularibus duplo longiora; achaenia piloso-ciliata aristis sursum ciliatis duplo longiora.

Shrub 1 m. high, trichotomously branched, glabrous throughout; stem terete, grayish-barked; branches and branchlets striate, scarcely angled, brownish, glaucescent; internodes 1–6 cm. long; leaves opposite; petioles slender, 4–10 mm. long, connate at base into a cup about 1 mm. high; blades usually cuneate or rhombic in outline, or lowest deltoid, 1.1–2.5 cm. long, 6–18 mm. wide, cuneately decurrent on petiole, usually 3- (rarely 4-) lobed about to middle or rarely nearly to base, lobes cuneate or oblanceolate to linear-lanceolate or lanceolate, mostly 6–16 mm. long, 1.5–3.5 mm. wide, acute, entire or terminal one (rarely also lateral) 2–3-dentate, thick, pale green, glaucescent; peduncles 1–4 at tips of branches, monocephalous, slender, glaucescent, usually naked, 1.5–5.5 cm. long; heads 1.2–2 cm. wide; disk 5–7 mm. high, about 7 mm. thick; involucre 4–6 mm. high, glabrous, glaucescent, outer phyllaries 8, herbaceous, narrowly triangular, obtuse, 3-nerved, 2–2.5 mm. long, 0.2–0.5 mm. wide, inner 8, submembranous, oblong, obtuse, obscurely ciliolate at apex, many-nerved, yellow-margined, glaucescent, about 1.8 mm. wide; rays 8, "orange yellow," neutral, tube sparsely pilosulous at apex, 1 mm. long, lamina oblong, subentire, 7.5 mm. long, 3.2 mm. wide, 8-nerved; disk corollas yellow, sparsely pilosulous at apex of tube, 3.2 mm. long (tube 1 mm., throat campanulate-funnelform, 1.6 mm., teeth ovate, 0.6 mm.); pales oblong, acutish or obtuse, about 5-nerved, pilose along midline, erose-spinulose at apex, 4.5 mm. long; ray achenes (inane) linear, sparsely pilose-ciliate; disk achenes obcompressed, obovate-oblong, 3.5–4 mm. long, 1.8 mm. wide, pilose-ciliate, ciliate at apex, sparsely pilose on midline inside; awns 2, lanceolate, upwardly ciliate, 1.5 mm. long; style tips deltoid, hispidulous, apiculate.

PERU: In the open formation, below Hacienda La Tahona, near Hualgayoc, Dept. Cajamarca, altitude 2600 m., May 15, 1904, *Weberbauer* 4048 (types in Herb. Berl.; photog. and fragm. in U.S. Nat. Herb., no. 1,194,714).

Related to *Coreopsis parviceps* Blake & Sherff, but decidedly glaucescent on the younger parts, and with less deeply divided leaves and much narrower outer phyllaries.

Coreopsis microlepis Blake & Sherff, sp. nov.—Frutex subglaber, caule tenui striato-angulato saepius simplice; folia opposita petiolata, lamina ambitu deltoidea paene ad costam trilobata, segmentis lateralibus cuneatis vel elliptico-obovatis integris vel 2–4-

dentatis apiculatis, terminali saepius ad medium 3-lobato; capitula mediocria 3–15 cymam vel paniculam nudam efficientia, rarius solitaria; involucri 6–7 mm. alti phyllaria exteriora ca. 8 ovata obtusiuscula glabriuscula interioribus triplo breviora; achaenia pilosa et ciliata aristis lanceolatis ciliatis triplo longiora.

Shrub 40 cm. high and more; stem usually simple below the inflorescence, rarely with few simple erect branches, 1.8 mm. thick or less, 6-angled, glabrous or slightly hispidulous in lines below the nodes, inflorescence rather sparsely hispidulous; internodes 1.3–5 cm. long, usually longer than leaves; leaves opposite, often with fascicles in their axils; petioles hirsute-ciliate chiefly toward base, slightly margined above, 4–10 mm. long, connate at base into a cup; blades deltoid in outline, 8–21 mm. long, 7–22 mm. wide, coriaceous, glabrous, somewhat thickened on margin, 3-lobed nearly to midrib (rachis 1 mm. wide or less), lateral segments cuneate, elliptic-obovate, or spatulate, 5–11 mm. long, 2–6 mm. wide, terminal segment 3–4-lobed usually about to middle, lobes entire or 2–3-toothed; upper leaves smaller, those subtending the branches of the inflorescence usually very small, subulate, entire; heads rather small, usually 3–15 in terminal cyme or panicle, on pedicels 1.5–5 cm. long; disk 6–7 mm. high, about 9 mm. thick; involucre 6–7 mm. high, glabrous or somewhat hispidulous at extreme base, outer phyllaries 8–9, ovate or oblong-ovate, thick-herbaceous, obtusish, 1.5–2 mm. long, 0.6–0.8 mm. wide, the inner 8, submembranous, elliptic-oblong, obtuse, about 2.2 mm. wide, blackish with narrow yellow margins; rays probably 8, neutral, golden yellow, tube sparsely pilose, 1.2 mm. long, lamina oval, subentire, 7-nerved, sparsely hirsutulous dorsally on chief nerves, 5.5 mm. long, 3 mm. wide; disk corollas golden yellow, glabrous, 3.3 mm. long (tube 1.1 mm., throat funnelform, 1.6 mm., teeth ovate, papillose-margined, 0.6 mm. long); pales obovate, obtuse to acute, about 6-nerved, pilose along midline, 4.5 mm. long; ray achenes (inane) linear, epappose, pilose-ciliate, glabrous on faces; disk achenes obcompressed, obovate to oblong, 2.8–3.5 mm. long, about 1.2 mm. wide, long-pilose-ciliate, pilose on both faces; awns 2, lanceolate, subpaleaceous, pilose-ciliate, persistent, 0.8–1.2 mm. long; style tips broadened, hispidulous, abruptly apiculate.

PERU: Province of Chachapoyas, 1835–6, *Mathews* 1418 (types in Herb. Kew; photog. and fragm. in U.S. Nat. Herb., no. 1,198,100).

Based on two sheets in the Kew Herbarium bearing six specimens, accompanied by several different labels, but all collected by *Mathews* in Chachapoyas and all clearly conspecific. The nearest allies of this species are *Coreopsis foliosa* Gray, which is similar in cutting of leaves, but has densely spreading-pilosulous stems and oblong rather densely pilosulous outer phyllaries 3.5–5 mm. long (GRAY'S types, in the Kew Herbarium, examined); *C. glaucodes*, which is glaucescent and has less deeply lobed leaves with fewer lobes, and very narrowly triangular outer phyllaries about half as long as the inner; and *C. parviceps*, which has fewer segments in the lower leaves, linear-elliptic and entire upper leaves, and linear-oblong outer phyllaries half as long as the inner. The specific name of the new species refers to the very small outer phyllaries.

Coreopsis polyactis Blake & Sherff, sp. nov.—Frutex densissime foliosus, ramis hirsutulis; folia opposita petiolata parva tripartita, segmentis saepius linearibus integris vel terminali tripartito; capitula brevissime pedunculata saepius solitaria majuscula; involucri ca. 1 cm. alti dense flavescenterque subtomentoso-pilosuli phyllaria interiora 13 exterioribus 11 ovatis distincte biseriatis subdimidio longiora; radii ca. 12; achaenia et aristae sursum ciliatae.

Shrub 1 m. high, trichotomous, densely leafy; branches subterete, sordid-hirsutulous chiefly in lines; internodes 4–10 mm. long; leaves opposite, usually with axillary fascicles; petioles 4–6 mm. long, somewhat ciliate, connate at base into hirsutulous cups 1 mm. high; blades deltoid in outline, 6–10 mm. long and about as wide, 3-parted, segments entire or terminal 3-parted, linear or narrowly linear-oblanceolate, 3–6 mm. long, 0.5–1 mm. wide, acute, thick, dark green, sparsely hirsutulous especially on margin; peduncles 1–3 at tips of branches, monocephalous, stout, densely and flavescently subtomentose-pilose, 1–1.8 cm. long, fistulose in age; heads 3–3.5 cm. wide; disk 1 cm. high, about 1.7 cm. thick; involucre 1–1.1 cm. high, densely and flavescently subtomentose-pilosulous, the outer phyllaries 11, distinctly biseriate, subequal, herbaceous, oval-ovate, obtuse, many-nerved, 6 mm. long, 3.3–4.8 mm. wide, the inner 13, thick-membranous, elliptic-oblong, narrowed to an obtuse or acutish apex, narrowly pale-margined, many-nerved; rays about 12, neutral, golden yellow, tube sparsely puberulous at apex, 2.5 mm. long, lamina oval, subentire, 10-nerved, 1.3 cm. long, 6.5 mm. wide; disk corollas yellow, apparently brownish-tipped, glabrous, ca. 4 mm.

long (tube 1.3 mm., throat funnelform, 2 mm., teeth ovate, 0.8 mm.); pales linear-oblong, 6 mm. long, acute, about 7-nerved, sparsely ciliolate above, pilose along midline; ray achenes (inane) glabrous, epappose; disk achenes (immature) linear-oblong, obcompressed, pilose-ciliate, pilose over whole inner face, glabrous on outer, not ciliate at apex; awns 2, lanceolate, upwardly ciliate, 3–4 mm. long; style tips deltoid, hispidulous, apiculate.

PERU: On grass steppes with scattered shrubs, between Hacienda Llaguén and Succhabamba, Dept. Libertad, Prov. Otuzco, altitude 3500–3600 m., June 28, 1914, *Weberbauer* 6995 (types in Herb. Berl. photog. and fragm. in U.S. Nat. Herb., no. 1,194,716).

Distinct from all other South American species in its broadly oval-ovate, biseriate outer phyllaries.

Coreopsis notha Blake & Sherff, sp. nov.—Frutex; rami striati sparse hispiduli; folia opposita ternatisecta, segmentis lateralibus 3–5-sectis terminali longiusculo stipitato pinnatim 5-secto, segmentis ultimis lanceolatis vel oblongis; capitula majuscula longe pedunculata; phyllaria interiora 8 elliptico-oblonga glabra exterioribus 6 oblongis basi ciliatis 4–5-plo longiora; achaenia piloso-ciliata aristis ciliatis duplo longiora.

Shrub 1 m. high, with long branches; stem striatulate, subterete, glabrescent or glabrate; branches striate-angulate, sparsely hispidulous; internodes mostly 1–4.5 cm. long; petioles sparsely ciliate, 1–1.5 cm. long, connate at base into somewhat hispidulous cups 1.5 mm. high; blades deltoid in outline, 1.8–2.7 cm. long and wide, ternatisect, basal segments short-stipitate or subsessile, 3–5-sect, the terminal long-stipitate, pinnately 5-sect with usually entire divisions, blade thickish, dark green, obscurely pubescent and ciliolate, ultimate segments lanceolate or oblong, acute, mostly 3–8 mm. long, 1–2.5 mm. wide; peduncles 1–3 at tips of stem and branches, 1 (rarely 2)-headed, sordidly crisped-pilosulous especially toward apex, naked or with few small bracts, 7–21 cm. long; heads 3.4–3.8 cm. wide; disk 7–8 mm. high, 8–11 mm. thick; involucre 9–12 mm. high, outer phyllaries constantly 6, herbaceous, oblong, 2–3 mm. long, 1–1.6 mm. wide, obtuse or rounded, somewhat ciliate at base, otherwise glabrous outside, inside sordid-pilosulous except toward apex, loose, inner phyllaries 8, membranous, oblong-elliptic,

9–12 mm. long, 3–4.6 mm. wide, obtuse, narrowly yellowish-margined, finely ciliolate at apex, otherwise glabrous; rays 8, neutral, "orange yellow," tube hispidulous, 2 mm. long, lamina oval, 1.5–2.1 cm. long, 9 mm. wide, subentire, 13–15-nerved; disk corollas yellow, hispidulous on tube and toward base of teeth, 5.8 mm. long (tube 1.8 mm., throat funnelform, 3 mm., teeth ovate, 1 mm.); pales oblong, 6–7 mm. long, hispidulous-ciliate at the truncate apex, pilose along midline of back, about 12-nerved; ray achenes (inane) linear, pilose-ciliate, sparsely pilose inside along midline; disk achenes linear-obovate, 6 mm. long, 1.7 mm. wide, obcompressed, pilose-ciliate, ciliolate at apex, pilose along midline inside; awns 2 (rarely 3), lance-linear, upwardly pilose-ciliate, 2.7–3.4 mm. long; style branches short-deltoid, hispidulous, apiculate.

PERU: Above San Pablo, Dept. Cajamarca, Prov. Cajamarca, altitude 2400–2700 m., April 26, 1904, *Weberbauer* 3812 (types in Herb. Berl.; photog. and fragm. in U.S. Nat. Herb., no. 1,194,719).

Nearest *C. spectabilis* Gray and *C. boliviana* Blake, but distinguished by its very short outer phyllaries and considerably broader ultimate lobes of leaves. Leaves similar to those of Mexican *C. rhyacophila* Greenm., but smaller and somewhat less dissected. Vernacular name is given as "pul," and the heads are said to be used for dyeing. As in all the other species here described (with the apparent exception of *C. glaucescens*, and perhaps also *C. microlepis*), the heads impart a rich orange color to the water in which they are boiled.

Coreopsis elgonensis, sp. nov.—Herba erecta, perennis, ramosa, 8–10 dm. alta; ramis angulatis, glabris, infra ligneis, internodis numerosis et saepe tantum 3–10 mm. longis. Folia opposita, numerosa, sessilia, tantum circ. 1 cm. longa, ternatim divisa, foliolis membranaceis, margine ciliatis, faciebus atro-punctatis et interdum sparsissime hispidis, cuneatis, ternatim lobatis vel integris, segmentis ultimis acerrime apiculatis, plerumque 2–3 mm. latis. Capitula pauca in corymbis disposita pedunculis 2–9 cm. longis, radiata, pansa ad anthesin 2.5–3.5 cm. lata et 8–11 mm. alta. Involucri bracteae exteriores 6–11, lineares, supra latiores, apice acutae, plerumque glabratae, 5–9 mm. longae; interiores lanceolatae, hispidae, paulo breviores. Flores ligulati 8–12, flavi, ligula anguste elliptico-oblanceolati, apice rotundati sed minute plus minusve denticulati, 8–12 mm. longi et 3–4.5 mm. lati. Achaenia late linearioblonga, plana, omnino atra, glabra, exaristata, 3.5–4.8 mm. longa et 1.1–1.3 mm. lata, marginibus non vere membranaceis.

R. A. Dummer 3304, locally frequent, in thicket, edge of cliff, west side of crater, alt. 13,000 feet, Mt. Elgon, Uganda, January, 1918 (type in Herb. Kew). A species strongly suggestive, in general habit, of certain South American species such as *Coreopsis polyactis* Blake and Sherff and *C. senaria* Blake and Sherff. The many small, sessile, cuneate, ternate or biternate leaves appear at first glance to be in whorls rather than in pairs. Correlated with the leaf abundance is the shortness of the internodes. Thus, for example, one branch of the type is seen to have 28 internodes in a length of 2.5 dm., giving an average length of only about 9 mm.

COREOPSIS BARTERI O. & H. Fl. Afr. Trop. **3**:390. 1877; *C. badia* Sherff, BOT. GAZ. **76**:90. 1923.

Recently I have had opportunity to compare the types of *Coreopsis Barteri* (Herb. Kew) and *C. badia* (Herb. Berl.) and found them to be identical. They are matched in turn by a third specimen, *W. B. Baikie*, banks of the Niger River, west tropical Africa (Herb. Kew). From the three specimens, the range is seen to extend from the Niger River southwest through Borgu (Bussango) into Togo.

COREOPSIS OCHRACEA O. Hoffm., Engler's Bot. Jahrb. **30**:431. 1901; *C. cosmophylla* Sherff, BOT. GAZ. **76**:90. *pl.* 9. *figs. h-n.* 1923; *Bidens ochracea* (O. Hoffm.) Sherff, *l.c.* 158.(pl. XIX).

HOFFMAN had not seen ripe fruits of this species.[2] In my own earlier studies it seemed that the specimens of this handsome species of the Nyassa region were of two kinds, differing generically on the basis of the winged character of the achenes. Further specimens have shown, however, that some material is merely more tardy than the rest in displaying achenial wings. As the specimens mature, their achenes become fairly well winged. Besides the type (*W. Goetze* 731, on red laterite, hilly plateau, in thin bush growth, at altitude of 1700 m., Bweni, Uhehe, March 11, 1899; Herb. Berl.), I have seen the following: *Ad. Stolz* 764, *pro parte*, growing 2 m. tall, at altitude of 600 m., Kyimbila, Langenburg, German East Africa, June 8, 1911 (Herb. Berl.); *idem* 764 *pro parte*, Kyimbila, at altitude of 600 m., February 27, 1912 (Herb. Deless.); *Muenzner* 159, Msamvia, Lake Tanganyika District, Germ. E. Afr., February 24, 1909 (Herb. Berl., type of *C. cosmophylla*); *A. Whyte*, northern Nyassaland (Herb. Kew); *E. Battiscombe* 83, at altitude of 3500–4000 feet, Muhoroni, Brit. E. Afr. (Herb. Kew; form with somewhat atypic foliage); *W. H. Nutt*, at about 6000 ft. altitude, between Lake Tanganyika and Lake Rukwa, in 1896 (Herb. Kew).

Coreopsis feruloides, sp. nov.—Herba erecta, ramosa, forsitan annua, circ. 7–10 dm. alta, glabra, viridis vel glaucescens, caule subtetragono. Folia sessilia vel subsessilia, 4–8 cm. longa, bi-

[2] "Reife Früchte fehlen; nach den Fruchtknoten zu erteilen könnten sie geflügelt sein"; Hoffm. *l.c.*

pinnata, costa mediana tenui, segmentis linearibus vel anguste lanceolatis, crassiusculis, minute ciliatis, obtusis vel subacutis, plerumque 2–4 mm. latis. Capitula subnumerosa, corymbosa, radiata, pansa ad anthesin 2.5–3 cm. lata et 5–7 mm. alta. Involucri subglabrati bracteae exteriores circ. 8, lineares, apice subobtusae indurataeque, 3–5 mm. longae, interiores lanceolatae circ. 6–7 mm. longae. Achaenia matura minuta, non exserta, atra, valde obcompressa, lineari-oblonga, leviter alata, faciebus subobscure striata, faciebus marginibusque minute erecto-setosa, corpore tantum 3.5–4 mm. longa et (alis inclusis) parce 1 mm. lata, apice biaristata; aristis tenuissimis, stramineis, setulis minutis erectis numerosis instructis, 1–1.6 mm. longis.

E. Battiscombe 945, at altitude of 7500–8000 feet, Kinabop Plateau, Western Aberdare Mountains, British East Africa (type in Herb. Kew).

The general habit simulates very closely that of the Mexican *Bidens grandiflora* Balb. and *B. ferulaefolia* (Jacq.) DC. The leaves suggest the primary lower lateral portion of the more decompound leaves of *Ferula glauca* L. Aside from the habit, the tiny achenes are very distinctive, very few African species of *Coreopsis* having such small ones. The achenial wings are of the same color as the body proper, thus easily escaping notice. The species is somewhat unwelcome, as it serves further to weaken the generic distinctions between *Coreopsis* and *Bidens*.

COSMOS SULPHUREUS var. LEIORHYNCHUS Griseb., descript. amplif.—Herba erecta, glabra, ±6 dm. (verisimiliter usque ad 1 m.) alta. Folia opposita, bipinnata vel tripinnata, principalia petiolo adjecto 6–11 cm. longa, petiolis 1.5–3 cm. longis, foliolis linearibus, apice acutis, margine integris sed minutissime spinuloso-ciliatis, non crassis, 1–4 mm. latis. Capitula ramos terminantia, subtenuiter pedunculata pedunculis 8–18 cm. longis, radiata, pansa ad anthesin circ. 3–3.5 cm. lata et 8–12 mm. alta. Involucri bracteae glabrae, exteriores circ. 8, lineari-subulatae, ad basim 1–1.5 mm. latae, e basi usque ad apicem acutum induratumque sensim angustatae, 5–8 mm. longae; interiores lanceolato-oblongae, paulo longiores. Flores ligulati 6–8, flavidi, ligula ovato-oblanceolati, apice subdenticulati, 10–14 mm. longi. Achaenia atra, lineari-fusiformia, obcompressa vel tetragona, manifeste 4-sulcata, glabra, supra ad apicem truncatum augustata, exaristata, 10–14 vel tantum 8 mm. longa et 1.5–2.2 mm. lata, cervice non perspicua.

Liberty H. Bailey[3] and *Ethel Zoe Bailey* 509, Los Charros, Venezuela, alt. 3000–3500 feet, December 27, 1920 (Herb. Field Mus.); *Mary Strong Clemens* 801, Camp Keithley, Lake Lanao, Mindanao, Philippine Islands, November, 1906 (Herb. Field Mus.); *J. Linden* 1510, savannahs, alt. 3000 ft., Valencia, State of Carabobo, Venezuela, December, 1843 (Herb. Deless.)

This variety, the type of which was collected by Dr. CRUEGER on the Island of Trinidad (*fide* Grisebach Fl. Brit. W. Ind. Isls. 374. [1861 *pagina cit.*]), has various points of similarity to *Cosmos bipinnatus* Cav., *C. caudatus* H.B.K., *C. sulphureus* Cav., and *C. Landii* Sherff. It differs from the first and second in having, among other characters, yellow rays; from the third in having smooth, short-necked achenes and lemon yellow or golden yellow (not reddish yellow) ligules;[4] from the fourth in having leaves of membranaceous texture. The Philippine specimen, although coming from a place widely remote from the type locality, appears to differ very slightly from the Venezuela material. Its leaves are mainly tripinnate instead of mainly bipinnate, and its achenes are 8–10 mm. rather than 10–14 mm. long. I have not seen GRISEBACH'S type, but he cited also "Venezuela," and it may well be that he had seen the *Linden* plant collected there a few years before.

Bidens calva (Schz. Bip.) C. B. Clarke (founded upon *R. F. Hohenacker* 344, near city of Mangalor, East India, in 1847) is a form likewise with exaristate, but with longer and more rostrate achenes. It has been referred by J. D. HOOKER (Fl. Brit. Ind. **3**:310. 1881) to *Cosmos sulphureus* Cav. The original specimens by HOHENACKER (Herb. Par., Herb. Deless., etc.), as well as several other sets of specimens examined by me, offer various intermediate aspects between typical *Cosmos sulphureus* Cav. and our plants, although the affinity with the latter is greater. Hence one cannot well assign to our plants, with their light yellow rays and exaristate, shorter, and less rostrate achenes, higher than varietal status.[5]

BIDENS PILOSA var. **calcicola** (Greenm.), comb. nov.; *Cosmos pilosus* H. B. K., Nov. Gen. et. Sp. **4**:241 (189). 1820; *Bidens rosea* Schz. Bip. *in* Seem. Bot. Voy. Herald 308. 1852–1857; *B. exaristata* DC. Prodr. **5**:600. 1836; *B. brachycarpa* DC. *l.c.*; *B. rosea* var. *calcicola* Greenm., Proc. Amer. Acad. **41**:264. 1905; *B. pilosa* var.

[3] I am indebted to Dr. BAILEY for having sent me this material.

[4] CAVANILLE'S employment of the name *sulphureus* was unfortunate. In the species *C. sulphureus* Cav. proper the rays are distinctly orange in color (*cf. C. aurantiacus* Klatt [Leopoldina **25**:105 1889], founded upon ordinary specimens of *Cosmos sulphureus* Cav., *Gust. Bernoulli*, in campis ad Tacotenango prope urbem Guatemala, Guat., December) and not yellow, as properly stated by GRISEBACH for the var. *leiorhynchus*.

[5] For the synonym *Bidens artemisiaefolius* var. *calvus* (Schz. Bip.) O. Ktze., which is invalid according to the Vienna Code, see O. KUNTZE, Rev. Gen. Pl. **1**:321. 1891.

brachycarpa (DC.) O. E. Schulz, Urban Symb. Antill. **7**:138. 1911.—Pl. XX.

GREENMAN (*l.c.*) lists *Palmer* 192, *E. W. Nelson* 6868, and *Heyde* and *Lux* 6172 (all in Herb. Gray) as representing *Bidens rosea* Schz. Bip. (*Cosmos pilosus* H.B.K.). Without discussing *B. rosea* Schz. Bip., the immature type of which (in Herb. Par.) is especially well matched by the *Palmer* plant, it is sufficient here to state that these specimens are referable to *Bidens brachycarpa* DC. The type and cotype specimens of *B. brachycarpa* DC. (Herb. Prodr. in Herb. Deless., Herb. Deless., Herb. Par., etc.), with their small leaves, small heads, more or less rosaceous ligules, and small, exaristate, upwardly attenuate achenes, appear widely different from typical *B. pilosa* L. A study of the various other herbarium specimens cited later, however, shows it to be utterly impossible to maintain separate specific rank for them; rather must they be given varietal rank under *B. pilosa* as was done by O. E. SCHULZ (*l.c.*). According to the Vienna Code, however, the earlier varietal name *calcicola* must be applied here. The type of the var. *calcicola*, *Pringle* 11340 (Herb. Gray) has a single pair of stem leaves present, these pinnately 5-parted, with the terminal and basal leaflets being more or less definitely 3-parted; the divisions are lanceolate; the involucres are rather densely canous-pubescent. These characters are found to be duplicated in various of the specimens cited below.

DeCandolle appears to have attached undue importance to the amount of scabridity on the achenial surfaces. Thus he placed *Berlandier* 5 and 113, with achenes scabrous, in his new species *B. brachycarpa*, but *Berlandier* 2220, with achenes less glabrous[6] and happening to have a taller, more corymbose habit, with the terminal leaflets more elongate, he described separately under the new name *B. exaristata*. The technical characters of flower and fruit offer no warrant for maintaining *B. exaristata* as a separate species or variety apart from the var. *calcicola*. As to the somewhat taller habit and more corymbosely or even fastigiately branched inflorescence observed in certain specimens (*Berlandier* 39, Herb. Deless., Herb. Drake *in* Herb. Par.; *idem* 2220, Herb. Deless., Herb. Drake *in* Herb. Par.; *Nelson* 2111, Herb. U.S. Nat.), these seem to be merely the result of a capricious growth. Indeed, *Berlandier* 800 and 2220 in the Gray Herbarium have a much more loosely corymbose inflorescence as, in fact, DECANDOLLE'S description states ("laxe corymbosa"), and thus at once remove from consideration the only character that by some botanists might be thought important. Through the first BERLANDIER specimen just cited (no. 800) an approach is made toward *B. pilosa* var. *bimucronata* (Turcz.) O. E. Schulz, a variety which has the heads usually larger, the leaves more often glabrous or subglabrous, and the lateral leaflets (in the variety proper) typically undivided.

Specimens examined: *Fr. Gerfroy Arsène*, alt. 2100 m., Punguábo, State of

[6] DECANDOLLE (*l.c.*) actually described the achenes as glabrous ("achaeniis glabris"), but in two sheets of *Berlandier* 2220 (Herb. Deless.) now before me, many of the achenes are distinctly scabrous near the apex.

Morelia, Mexico, October 17, 1909 (Herb. Deless.); *Berlandier* 5 and 113, Tampico, State of Tamaulipas, Mexico, in 1827 (Herb. DC. Prodr.; Herb. Deless.; Herb. Par.; Herb. Webb); *idem* 39, Mexico (Herb. Par.); *idem* 800, Mexico (Herb. Gray); *idem* 2220, between Victoria and Tula, Mexico, November 1830 (Herb. DC. Prodr.; Herb. Deless.; Herb. Gray; Herb. Par.); *Bourgeau* 2253, Valley of Cordova, Mexico, April 16, 1866 (Herb. Par.); *Prof. A. Dugès*, in garden near Guanajuato, State of Guanajuato, Mexico, in 1891 (Herb. Gray); *Carl Heller* 37, alt. 3000 ft., in meadows, Mirador, State of Vera Cruz, Mexico (Herb. Par.; Herb. Mus. Vienna); *Heyde and Lux* 3788, alt. 3500 ft., Cerro Gordo, Dept. Santa Rosa, Guatemala, September 1892 (Herb. Mun.); *idem* 6172, alt. 800 m., Cuijiniquilapa, Dept. Santa Rosa, Guatemala, November 1893 (Herb. Boiss.; Herb. Brit. Mus.; Herb. Field Mus.; Herb. Gray); *Dr. H. Karsten*, Quindio, Colombia (Herb. Petrop.); *E. Kerber* 9, Cordoba, State of Vera Cruz, Mexico, July 22, 1882 (Herb. Boiss.; Herb. Brit. Mus.; Herb. Copenh.; Herb. Deless.; Herb. Mun.; Herb. Par., 3 sheets; Herb. Mus. Vienna, etc.); *Liebmann* 640, Colipa, State of Vera Cruz, Mexico, March 1841 (Herb. Copenh., 2 sheets); *idem* 641, Papantla, State of Vera Cruz, Mexico, June 1841 (Herb. Copenh.); *idem* 643, Mirador, State of Vera Cruz, January 1843 (Herb. Copenh.); *idem* 651, Tehuacan, State of Puebla, Mexico, December 1841 (Herb. Copenh.); *Fred Müller* 238, Orizaba, State of Vera Cruz, Mexico, in 1853 (Herb. N.Y. Bot. Gard.); *E. W. Nelson* 2111, alt. 4500–5700 ft., between Tlapa and Ayusinapa, State of Guerrero, Mexico, December 13, 1894 (Herb. Gray); *idem* 6868, Los Reyes, State of Michoacan, Mexico, February 8–12, 1903 (Herb. Gray, foliis glabris et valde membranaceis); *Fr. Nicholas*, bank of the Atoyac River near Puebla, State of Puebla, Mexico, July 15, 1909 (Herb. Mun.); *idem* 5, Teocalli de Choluca, State of Puebla, Mexico, December 1911 (Herb. Deless.); *Dr. Edward Palmer* 68, alt. circ. 15 m., vicinity of Tampico, State of Tamaulipas, Mexico, January 1910 (Herb. Mo. Bot. Gard.).

BIDENS PILOSA CALCICOLA **dissecta**, f. nov.—A varietate differt: foliis bipinnatis vel etiam tripinnatisectis, segmentis linearibus vel anguste lanceolatis.

Specimens examined: *Fr. Gerfroy Arsène* 11, alt. 2000 m., Loma S. Maria, State of Morelia, Mexico, September 4, 1910 (Herb. Deless., foliis glabratis, valde membranaceis); *Heyde and Lux* 6164, alt. 1300 m., Malpais, Dept. Santa Rosa, Guatemala, November 1893 (Herb. Berl., 2 sheets; Herb. Boiss., 4 sheets; Herb. Brit. Mus.; Herb. Copenh.; Herb. Field Mus.; Herb. Gray, type; Herb. Kew); *iidem* 6170, alt. 1600 m., La Vega, Dept. Santa Rosa, Guatemala, September 1893 (Herb. Berl.; Herb. Boiss.; Herb. Brit. Mus.; Herb. Gray; Herb. Kew); *Schaffner*, Mexico (Herb. Berl.); *Cacc. and Ed. Seler* 1184, Patzcuaro, State of Michoacan, Mexico, November 2, 1895 (Herb. N.Y. Bot. Gard.).

A form comparable with the variety *calcicola* in much the same way that the bipinnately leaved form (to be discussed later) of *B. pilosa* var. *bimucronata* (Turcz.) O. E. Schulz is comparable with that variety. Indeed, of the var.

bimucronata and its form with more compound foliage, there are found at times stunted or dwarfed specimens which have flowering and fruiting heads diminutive enough to be taken for var. *calcicola* and f. *dissecta*. It is therefore possible that in some of my past herbarium determinations I may have confused the two varieties and their respective forms to a slight extent.[7]

BIDENS ANDICOLA **Mandonii,** var. nov.—A specie differt: saepius annua, altior (usque ad 8 vel 10 dm. alta), minus ramosa et magis attenuata, capitulis ad anthesin subradiatis, minoribus, tantum circ. 5 mm. latis et 5–7 mm. altis, achaeniis gracilioribus.

Specimens examined: *G. Mandon* 48 (type) and 44 *pro parte*, in uncultivated places, alt. 2650 m., vicinity of Sorata (San Pedro), Bolivia, March 1859 (Herb. Boiss.; Herb. Brit. Mus.; Herb. Deless.; Herb. Kew; Herb. Par.; Herb. Mus. Vienna).

M. GUSTAVE BEAUVERD, in 1919, had referred my type (Herb. Boiss.) doubtfully to a variety of *B. pilosa* L. The fruiting heads, however, are more those of *B. andicola* H.B.K. *Mandon* 44, collected at the same time and place (Herb. Brit. Mus., Herb. Kew, Herb. Mus. Vienna), offers several transitional forms that connect this variety satisfactorily with typical *B. andicola*. In fact the Boissier Herbarium specimen of *Mandon* 44 and one in the Museum at Vienna are closer to the variety than to the species proper.

BIDENS VULGATA **dissectior,** var. nov.—A specie differt: foliis principalibus bipinnatis vel tripinnatisectis.

E. Bourgeau (Palliser's Brit. N. Amer. Expl. Exped.), willow marsh at edge of Saskatchewan River, Saskatchewan, September 18, 1857 (Herb. Par., type; Herb. Kew).

BIDENS ANTHRISCOIDES **decomposita,** var. nov.—A specie differt: foliis bipinnatis.

C. G. Pringle 11822 *pro parte*, Barranca near Guadalajara, Jalisco, Mexico, October 17, 1903 (Herb. Kew, type; Herb. Berl.; Herb. Gray; Herb. U.S. Nat.).

Pringle 11822 in the Herbarium of Field Museum has the leaves tripartite and matches the type material of *Bidens anthriscoides* DC. (*Berlandier* 1010, Herb. Deless.; Herb. Brit. Mus.; Herb. Par.) fairly well except in being glabrate. Elsewhere, the specimens of *Pringle* 11822 are seen to have delicately bipinnate leaves, similar to those of *Bidens odorata* Cav. Through this form, apparently best regarded as a variety, *B. anthriscoides* DC. is found to be rather closely related to *B. inermis* Wats.

BIDENS REMYI (Hillebr.) Sherff, BOT. GAZ. **70**:97. 1920; *Campylotheca Remyi* Hillebr. Fl. Hawaiian Isls. 212. 1888; *Coreopsis*

[7] For var. *calcicola* and f. *dissecta* I have, in the various herbaria, used previously the name *B. pilosa* var. *brachycarpa* (D.C) O. E. Schz., etc.

Hillebrandiana Drake del Cast. Illustr. Fl. Ins. Mar. Pacif. 209. 1890; *Campylotheca rutifolia* Lévl., Fedde Repert. Spec. Nov. **10**: 123. 1911.

LÉVEILLÉ'S *Campylotheca rutifolia* was based upon *Abbé Urbain Faurie* 931, Wailau, Molokai, Hawaiian Islands, June 1910 and *idem* 965, Hawaiian Islands, in 1909. Both of FAURIE'S numbers have been examined by me (no. 931, Herb. Brit. Mus. and Herb. Par.; no. 965, Herb. Brit. Mus.). They match perfectly the type material (Herb. Gray) of *Bidens Remyi* (Hillebr.) Sherff, to which they must be referred.

BIDENS MAUIENSIS **lanaiensis** var. primum nominat.; *Campylotheca mauiensis* var. β (*sine nom.*) Hillebrand Fl. Hawaiian Isls. 213. 1888.—Var. foliis validius membranaceis, saepe validius divisa, petiolis tenuibus usque ad 5 cm. longis; capitulis minoribus, pansis ad anthesin circ. 1.2–1.5 cm. latis; bracteis exterioribus minoribus; floribus ligulatis plerumque tantum 5 vel 6; achaeniis brevioribus 5–7 mm. longis, atris, plano-convexis vel etiam subtetragonis, nunc anguste alatis nunc exalatis, apice exaristatis sed minute coronulatis.

Dr. William Hillebrand, Island of Lanai, Hawaiian Islands, in 1879 (Herb. Gray, type); *idem*, Lanai, July 1870 (Herb. Brit. Mus.; Herb. Kew); *idem*, northern Maui, Hawaiian Islands (Herb. Brit. Mus.); *G. C. Munro* 450 and 451, Maunalei, Lanai, April 19, 1915 (Herb. Brit. Mus.).

The specimens from Lanai, as also the *Hillebrand* specimen from "northern Maui," are of the same general habit as the typical *B. mauiensis* (Gray) Sherff from Maui, but in respect to the characters noted are definitely marked. It will be observed that there are more pronounced differences than are found to occur in certain other cases between two accepted species (for example, *Bidens connata* Muhl. and *B. comosa* [Gray] Wieg.; *B. pilosa* L. and *B. chinensis* [L.] Willd.). In the case at hand, however, the remarkable degree of endemism displayed by Hawaiian plants renders the value of these distinguishing characters somewhat uncertain. For the present, I have thought it wisest to follow the treatment of HILLEBRAND and also of the late C. N. FORBES (*cf.* SHERFF, BOT. GAZ. **70**:98. 1920), both of whom regarded the Lanai material as representing a variety or varieties of *B. mauiensis*.

COSMOS PURPUREUS (DC.) Benth. and Hook. Gen. Pl. **2**:387. 1876; Hemsl. Biol. Centr. Amer. Bot. **2**:200. 1881; *Bidens purpurea* DC., *cum* var. *glabriuscula* DC. Prodr. **5**:604. 1836; *Coreopsis purpurea* Moc. Sess. ex DC. *l.c.*; *Cosmos Uhdeanus* Kunth, Ind. Sem. Hort. Berol. 1846 Coll. 12; Walp. Repert. **6**:721. 1847.

The original material of *Cosmos Uhdeanus* Kth. has not been seen by me, but the description is fairly satisfactory and leaves no doubt as to which of the species of *Cosmos* was intended. ROBINSON (Proc. Amer. Acad. **44**:623. 1909) has properly associated with this name *Pringle* 8238, a handsome plant liberally represented in the larger herbaria, and matched, further, by a beautiful specimen collected more recently by Adole at Vera Cruz (Herb. Field Mus.).

Bidens purpurea DC. and its var. *glabriuscula* DC.[8] were founded respectively upon *Berlandier* 1007 and *Berlandier* 1021 [*pro parte*]. These numbers, also *Berlandier* 985 and 1163, are especially well represented in the valuable herbarium left by MOÏSE ETIENNE MORICAND (and now in Herb. Deless.). Excluding one sheet of no. 1021, which is typical *Cosmos scabiosoides* H.B.K., the rest show various intergradations from small leaves 2–3 cm. long, pinnatisect as described by DECANDOLLE, to larger leaves 6–8.5 cm. long, definitely bipinnate and matching those of the *Pringle* and the *Adole* plants. Thus *Cosmos Uhdeanus* Kunth, typified as it appears to be by *Pringle* 8238 and by the *Adole* plant, is found synonymous with and referable to *Cosmos purpureus* (Kth.) B. & H.

From *Cosmos purpureus*, *C. scabiosoides* is seen to differ in having the rays usually (though by no means always) a darker purple, often almost black; the disk florets bright yellow except for the purple teeth (in *C. purpureus* the disc florets are entirely dark purple or sometimes yellowish merely at the base); the mature achenes long-attenuate above, not obscurely cervicate or even of full thickness; the less compound leaves dull-colored, apparently thickish, not thinnish, not light bright green above nor tending to a reddish brown below (against which, in *C. purpureus*, the white, stiff hairs appear, under a lens, in sharp contrast).[9]

Specimens examined: *Brother Adole*, Vera Cruz, Mexico, October 1910 (Herb. Field Mus.); *Berlandier* 985, Cordillera de Guchilaque, Mexico (Herb. Deless.); *idem* 1007, west of the Cordillera de Guchilaque, Mexico, October 1827 (Herb. Brit. Mus.; Herb. Deless., 3 sheets; type and cotypes); *idem* 1021 *pro parte*, Cordillera de Guchilaque, Mexico, October 1827 (Herb. Deless.); *idem* 1163, Toluca, State of Mexico, Mexico (Herb. Deless.); *C. G. Pringle* 8238, alt. 6500 ft., mountains above Cuernavaca, Morelos, Mexico, September 30, 1899 (Herb. Field Mus.; Herb. Univ. Vienna).

[8] The var. *glabriuscula* was merely a subglabrous variant and does not appear to merit segregation, even as a *forma*.

[9] Specimens of *Cosmos scabiosoides* H.B.K. recently examined: *Berlandier* 1021 *pro parte*, Cordillera de Guchilaque, Mexico (Herb. Deless.); *E. Bourgeau* 2930, Escamella, Vera Cruz, Mexico, September 1–2, 1866 (Herb. Deless., 2 sheets; Herb. Univ. Vienna); *C. A. Purpus* 1551, hillsides, open woods, alt. 7000–8000 ft., Salto de Agua, Mexico, November 1905 (Herb. Field. Mus; Herb. Univ. Vienna, 2 sheets); *C. G. Pringle* 4263, hills of Patzcuaro (type locality), Michoacan, Mexico, October 11, 1892 (Herb. Field Mus., 3 sheets; Herb. Univ. Vienna, simple-leaved state, f. *indivisus* Robinson); *idem* 9888, alt. 8500 ft., hills near Ozumba, State of Mexico, Mexico, November 4, 1902 (Herb. Field Mus.).

BIDENS TRIPLINERVIA H.B.K. Nov. Gen. et Sp. **4**:231 (182). 1820; *B. serrata* Pav. *ex* DC. Prodr. **5**:597. 1836.

To *Bidens triplinervia* H.B.K.. which I have already discussed rather fully (BOT. GAZ. **76**:155. 1923), must be referred *B. serrata* Pav. *ex* DC. The type (no. 977 of the Ruiz, Pavon, and Dombey expedition, Peru, in 1788; *cf.* LASÈGUE, Mus. Bot. Deless. 244–247. 1845) is extant in the DeCandolle Prodromus Herbarium (Herb. Deless.). It lacks flowers, as stated by DE CANDOLLE, but is seen to be merely a form of *B. triplinervia* with some leaves undivided and lanceolate or narrowly oblong; others somewhat incised or lobed at the base.

BIDENS TRIPLINERVIA var. **macrantha** (Wedd.), comb. nov.; *B. glaberrima* DC. Prodr. **5**:601. 1836; *B. humilis* var. *macrantha* Weddel Chlor. And. **1**:69. 1856.

In the long list of additional names already given by me (BOT. GAZ. **76**:155. 1923) as referable to *Bidens triplinervia* H.B.K., it is seen that the majority refer to forms with leaves at least bipinnately compound. The simple-leaved form, described under the names *B. triplinervia* H.B.K., *B. hirtella* H.B.K., *B. procumbens* H.B.K., *B. serrata* Pav. *ex* DC., and *B. affinis* Kl. and O., is rather rare.[10] The form with mostly bipinnate or tripinnate leaves is the one indicated under *B. crithmifolia* H.B.K., *B. delphinifolia* H.B.K., *B. humilis* H.B.K., *B. artemisiaefolia* Poepp. and Endl., *B. consolidaefolia* Turcz., *B. humilis* vars. *macrantha* Wedd. and *major* Schz. Bip., *B. decomposita* var. *hirsutior* C. B. Clarke, *B. humilis* var. *tenuifolia* Schz. Bip. *ex* Griseb., *B. pilosa* var. *discoidea* subvar. *decomposita* f. *hirsutior* O. Ktze. (Rev. Gen. **1**:322. 1891), *B. grandiflora*

[10] *B. hirtella* H.B.K. (Pl. XXI) was based upon a specimen from an unknown locality, but with undivided though narrower leaves: "Folia opposita, petiolata, lanceolata, acuta, serrata, basim versus subincisa, in petiolum angustata et integerrima, reticulato-venosa, membranacea, utrinque hirta, subtus pallidiora, subpollicaria. Petioli duas lineas longi, pubescenti-hirti, basi dilatati et connati . . . . folia nec triplinervia sunt." KUNTH's type (Herb. Par.) does have the leaves with a distinct suggestion of two lateral nerves running nearly half-way up the blade, giving a somewhat triplinervate appearance. BONPLAND gave an extra specimen to the Paris Herbarium under the name *B. hirtella* H.B.K. This was from Chillo, Ecuador ("Chillo, villa generosissimi Marchionis de Selvalegre" H.B.K. *l.c.* **7**:380. 1825) and the leaves exactly match those of the type material of *B. triplinervia* H.B.K., not of *B. hirtella* H.B.K.

B. procumbens H.B.K. was described likewise from a narrower-leaved form: "Folia opposita, petiolata, lanceolata, acuta, serrata, basi angustata et integerrima, reticulato-venosa, subtriplinervia, membranacea, utrinque hispidula, subtus pallidiora, adjecto petiolo subsesquipollicaria; inferiora multo minora, magis approximata. Petioli subciliati." The type sheet (Herb. Par.) is accompanied by an extra sheet with one small plant. This has leaves more ovate, approaching those typical for *B. triplinervia*, the rays are about five as in the type, and the label says, "Bidens procumbens varietas?"

var. *humilis* (H.B.K.) O. Ktze. (*l.c.* 3[II]:136. 1898) and *B. attenuata* Sherff.[11] My recent examination of the type of *Bidens glaberrima* DC. (Herb. Prodr. in Herb. Deless.) revealed once again a mere compound-leaved form ("foliis oppositis petiolatis pinnato-multifidis intermedio multo longioribus, lobis oblongo-linearibus crassiusculis," DC. *l.c.*) of *B. triplinervia* H.B.K.[12]

A study of several hundred specimens of this species indicates such a wide range of variation in height of plants, amount of pubescence, form and size of leaves and size of flowering heads, that attempts at fine distinctions prove fruitless. In a broad way, however, the species may be divided into three major divisions upon the basis of the simplicity or the compoundness of the leaves. The first, already mentioned for typical *B. triplinervia*, is characterized by having the leaves all or mainly simple, usually ovate or ovate-lanceolate, rarely linear-lanceolate. The second, apparently first described with varietal rank by WEDDELL (*l.c.*),[13] is the second form just given, represented by the synonyms *B. crithmifolia*, *B. delphinifolia*, etc., and including *B. glaberrima* DC. It may be known as *B. triplinervia* var. *macrantha* (Wedd.). The third, like the first rather rare comparatively, has the leaves tripartite, with usually ovate and nearly always very pubescent leaflets. It thus stands, in leaf form, intermediately between the first two kinds. It is the *Bidens mollis* of POEPPIG and ENDLICHER (Nov. Gen. et Sp. 3:49. 1845), and may more properly be taken as:

BIDENS TRIPLINERVIA var. **mollis** (Poepp. and Endl.), comb. nov. (Pl. XXII figs. *a–i*)—Folia tripartita, saepius molliter pubescenti-villosa et subcanescentia, foliolis serratis, lateralibus plerumque ovatis, abrupte in basim sessilem contractis, terminali majore, oblongo-ovato vel rhomboideo-ovato.

[11] Pl. XXII figs, *j–p*. At the time that *B. attenuata* originally was described (from Ghiesbreght 85, *pro parte*), *B. triplinervia* var. *macrantha* or its synonyms were commonly restricted by botanists to South American specimens. I have since found abundant material from Guatemala (*Salvin*, Volcan de Fuego) and Mexico (*Ghiesbreght* 85, 533, etc., Chiapas; *Cuming* 53, Oaxaca; *Galeotti* 2021 and 2067, Oaxaca; *Pringle* 4915, Oaxaca; *Sallé* 91, Oaxaca; *Galeotti* 2169, Vera Cruz; *Linden* 491, Vera Cruz; *Palmer* 2062, Coahuila) which is inseparable from the South American material and shows a more northern range than formerly supposed. Among the Mexican specimens studied are several which display more or less pronounced transitions from the typical form to *B. attenuata* and reveal the latter to be merely an attenuated form with the five rays rather large and the almost flagelliform leaflets more or less convolute.

[12] It will be observed that *B. glaberrima* DC. is widely different from *Cosmos Landii* Sherff (*Bidens Palmeri* Gray) to which A. GRAY (Proc. Amer. Acad. 22:429. 1887) apparently had suspected it of belonging.

[13] WEDDELL'S type was *William Jameson* 55, alt. 13,000 ft., on rocks, Pichincha Mts., Ecuador, January 21, 1856. Certain other specimens by Jameson were 8-rayed, and thus approached somewhat *B. andicola* H.B.K. *Jameson* 55, however, is very definitely 5-rayed at Kew and at Geneva. In London (Herb. Brit. Mus.) one of the heads has 7 rays.

Specimens of var. *mollis* examined (partial list): *Gust. Bernoulli* 155, dry place, Calvario, Guatemala, November 1865 (Herb. Deless.); *F. C. Lehmann* 357, at edges of woods and open forest places, alt. 2000 m., Tunguragua River, Peru, October 31, 1879 (Herb. Boiss.; Herb. Kew); *idem* 433, alt. 2000 m., arid valley of Baños, Tunguragua River, Peru, December 13, 1880 (Herb. Boiss.); *idem* 1608, damp places, alt. 2000 m., San Marcos, Guatemala, June 17, 1884 (Herb. Boiss., more robust form 6 dm. high, the leaflets 3–5 cm. long); *idem* 2835, above Pais Camba on the Sotorá, alt. 2600–3000 m., Cauca, Colombia, May 6, 1883 (Herb. Berl.; Herb. Boiss.); *idem* 3511, alt. 2650 m., Cauca, Colombia, February 1, 1884 (Herb. Boiss.; Herb. Brit. Mus.); *G. Mandon* 43 *pro parte*, in uncultivated places, on hills etc., alt. 2600–2700 m., Espada Munaypata, San Pedro, vicinity of Sorata, Bolivia, March, 1859 (Herb. Deless., 2 sheets); *idem* 43 *pro parte*, everywhere in dry, rocky, uncultivated places etc., alt. 2650–3200 m., vicinity of Sorata, Bolivia, February–May 1859 (Herb. Boiss.; Herb. Brit. Mus.; Herb. Deless.; Herb. Par.; Herb. Mus. Vienna); *idem* 46 *pro parte*, slopes of hills, uncultivated places etc., alt. 2800 m., vicinity of Sorata, Bolivia, March 1859 (Herb. Boiss.; *alibi est* var. *macrantha*); Mathews, vicinity of Chachapoyas, Peru (Herb. Kew, form with achenes all exaristate; Herb. Deless., 2 sheets); *Eduard Poeppig* 1377, open, warm places, calcareous mountains at Cassapi, Peru, September 1829 (Herb. Mus. Vienna, type); *R. Spruce* 5047, at foot of Mt. Tunguragua, Ecuador, 1857–1859 (Herb. Boiss.; Herb. Brit. Mus.; Herb. Copenh.; Herb. Deless., 2 sheets; Herb. Kew, 2 sheets; Herb. Par.; Herb. Petrop.; Herb. Mus. Vienna).

BIDENS SPECIOSA var. PATULA (Gardn.) O. E. Schulz, Urban Symb. Antill. **7**:142. 1911; *B. patula* Gardn., Hook. Lond. Jour. Bot. **7**:405. 1848; *B. longipetiolata* Rusby, Bull. N. Y. Bot. Gard. **8**:131. 1912.

B. patula Gardn., correctly referred by O. E. SCHULZ to a variety of *B. speciosa*, differs from *B. speciosa* proper in having the leaves all simple, ovate-lanceolate, up to 5.5 cm. wide. *B. longipetiolata* Rusby (*R. S. Williams* 194, alt. 3800 ft., Mychariapo, Bolivia, April 9, 1902; Herb. Brit. Mus.; Herb. N.Y. Bot. Gard., type) is seen to be a form of the var. *patula*, differing in having the somewhat longer petioles measuring up to 4.5 cm. in length.

Bidens Oerstediana (Benth. *ex* Oerst.), comb. nov.; *Coreopsis Oerstediana* Benth. *ex* Oerst., Vidensk. Meddel. Kjöbenh. 1852:93. 1852.

This species from Nicaragua[14] was collected by OERSTED "in monte Masaÿa . . . . 1851." It does not appear to have been collected since then. In fact, the region around Masaÿa, in western Nicaragua, has been explored botanically very little. The type specimen at Kew[15] is a slender, herbaceous plant, quite un-

[14] Not Brazil, as stated in the Index Kewensis.

[15] The OERSTED plants, generously loaned to me from the Herbarium of the University of Copenhagen by Dr. CARL CHRISTENSEN, do not appear to have among them a duplicate of this species.

like the fruticose species so commonly found in Mexico and Central America for true *Coreopsis*. BENTHAM's original description likened it to some species of *Bidens*, but withheld it from *Bidens* because of the upwardly barbed achenial aristae. The young achenes were described as *subalata*. The type specimen, though slightly immature in its achenes, is of a plant related to *Bidens coronata* (L.) Britton (*B. trichosperma* Michx.) of the northeastern United States. Its achenes are somewhat immature, but are not more plainly margined or subwinged than the average *Bidens* achenes of similar stage of maturity.[16]

BIDENS INVOLUCRATA **retrorsa,** var. nov.—A specie differt: achaeniorum aristis retrorsum hamosis.

B. F. Bush 5175 *pro parte*, Webb City, Missouri, September 25, 1908 (Herb. Gray, type; *non in* Herb. N.Y. Bot. Gard., *quo idem* 5175 *B. aristosa est*).

Several American species of *Bidens* have been shown to have a more or less definitely pronounced form with achenial awns barbed in the opposite way to that for those of the typical form. Thus we have *B. frondosa* var. *anomala* Port. *ex* Fern., *B. aristosa* var. *Fritcheyi* Fern., and *B. heterodoxa* var. *orthodoxa* Fern. With a very few species of *Bidens*, such as *B. ambigua* S. Moore of Africa, the direction of the barbs on the aristae appears to vary somewhat indiscriminately. For the species of the United States and Canada the direction appears more definitely fixed, however, and its reversal, noted in certain often widely scattered localities, may afford, as held by FERNALD,[17] the basis for legitimate varietal segregation. In accordance with FERNALD's view, the rare form of *B. involucrata* collected by BUSH is named var. *retrorsa*.[18]

BIDENS FRONDOSA var. **pallida** (Wieg.), comb. nov.; *B. melanocarpa* var. *pallida* Wieg., Bull. Torr. Bot. Club **26**:406. 1899.

When WIEGAND's *Bidens melanocarpa* was shown by E. L. GREENE (Pittonia **4**:246–250. 1901) to be identical with and referable to *B. frondosa* L., the var. *pallida* was overlooked. I have had no opportunity of repeating WIEGAND's field studies of this interesting form, and so rely upon his judgment as to its varietal status. In the scanty herbarium material examined by me, however, it had seemed that extended field observations might indicate a somewhat lower than varietal rank as ordinarily interpreted.

BIDENS MICRANTHA var. **laciniata** (Hillebr.), comb. nov.; *Campylotheca micrantha* var. *laciniata* Hillebr. Fl. Hawaiian Isls. 216.

[16] Dr. S. F. BLAKE, of the U.S. Bureau of Plant Industry, has kindly examined the type and likewise concluded that the plant was closer to *Bidens* than to *Coreopsis*.

[17] See also Wiegand, Bull. Torr. Bot. Club **26**:400–401. 1899.

[18] For those who refuse to abide by the unfortunate provision, Article 50, of the Vienna Code (permitting a name to stand when there exists "an earlier homonym which is universally regarded as invalid"), the name becomes *Bidens polylepis* var. *retrorsa* (*cf.* Sherff, BOT. GAZ. **76**:160. 1923).

1888.—A form fairly well marked but not enough to merit separate specific rank.

The earlier binomial *Bidens micrantha* Gaud. is used here since the genus *Campylotheca*, as I have previously stated (Bot. Gaz. **70**:91–96. 1920), does not appear to me worthy of retention.

Bidens pilosa var. **minor** (Bl.), comb. nov.; *Kerneria dubia* Cass., Dict. Sc. Nat. **24**:398. 1822 (*pro parte*); *Bidens sundaica* Blume *et* var. *minor* Blume Bijdr. 913. 1826; *B. leucantha* var. *sundaica* (Bl.) Hasskarl, Cat. Pl. Hort. Bog. 100. 1844; *etiam in* Miquel Fl. Ned. **2**:77. 1856–1859; *B. aurantiaca* Colenso, Trans. New Zeal. Inst. **27**:388. 1895; *B. pilosa* var. *dubia* (Cass.) O. E. Schulz, Urban Symb. Antill. **7**:135. 1911.

Bidens pilosa L. has among its various varieties and forms a subradiate variety, widely distributed in both hemispheres. It apparently was first observed by Cassini.[19] O. E. Schulz (*l.c.*) has employed for it the varietal name *dubia*, but the synonymous *Bidens sundaica* Bl. had already been reduced to varietal rank by Hasskarl (*l.c.*) in 1844, and so takes precedence over the name *dubia*. In his original description, however, Blume (*l.c.*) listed a variety *minor*, "caule foliisque humilioribus. Crescit: cum praecedente [i.e., *B. sundaica ips.*, prope Buitenzorg, Java]." Recently, through the great kindness of Dr. J. W. C. Goethart, Director of the Rijks Herbarium at Leyden, I was privileged to examine early specimens by Blume and by Junghuhn, from Java. Three sheets (nos. 900,146 . . . . 72 [*pro parte*]; 900,146 . . . . 73; 900,146 . . . . 75) bear excellent specimens of Blume's *Bidens sundaica*. A few minute rays are present. The first of these sheets bears also the basal part of a specimen (and, in addition, a fruiting branch which probably belonged to it), labeled unmistakably in Blume's own handwriting, "*Bidens Sundaica Variet.*" Dr. Goethart (*in litt.*) very properly regards this as "probably type of var. *minor*." The one fruiting head still attached to the rather depauperate basal portion exactly matches the others on the *B. sundaica* plants. A fourth sheet bears still more depauperate material collected by Dr. Fr. Junghuhn, no. 357, on Mt. Dieng, Java. It is labeled in Miquel's[20] handwriting (*fide* Goethart *in litt.*) as a depauperate *forma* of *B. sun-*

[19] ". . . . les calathides, composées d'un disque jaune et d'une couronne blanchâtre, sont larges de cinq lignes. . . . . Nous avons observé, pendant plusiers années, des individus vivans de cette espèce, cultivés au Jardin du Roi, et nous avons remarqué que leurs calathides etoient le plus souvent incouronnées, rarement radiées. Dans ce dernier cas, la couronne étoit composée de cinq à sept fleurs, dont la corolle avoit le tube court, et la languette courte, large, orbiculaire, tridentée au sommet, multinervée, a nervures jaunâtres . . . . ," Cassini, *l.c.*

[20] Miquel (*l.c.*) cites a depauperate form collected by Junghuhn: "*B. leucantha β sundaica* Hassk. *l.c.* p. 100, cujus auctoritate formam hanc alioquin satis constantem huc retuli.—Formam omnibus partibus depauperatam in elevatioribus montanis Javae insulae cl. Jungh. legit."

daica Bl. Indeed, its three specimens (one of them, in flower, having the tiny rays very evident) are so obviously a merely less developed form of *B. sundaica*, that few if any authors today would seek to draw any distinctions.

It is evident, then, that the actually equivalent name *minor*, given varietal status long before the name *sundaica*, must in turn take precedence, supplanting both *sundaica* and *dubia*.[21]

BLUME's description, "B. floribus subradiatis . . . ." is matched by upward of a thousand specimens examined by me in the past few years.[22] It is represented in particular by several of BLUME's own specimens in Herb. Brit. Mus. (where numbered 139), Herb. DC. Prodr. (*in* Herb. Deless.), Herb. Par., and Herb. Webb. In the last three herbaria the heads are mostly rayless, perhaps having had the few rays removed in previous examinations. The foliage aspect, however, is definitely that of the ordinary subradiate variety. Furthermore, the plant at the British Museum (of Natural History) is definitely subligulate.[23]

Bidens aurantiaca Colenso has its description ("Florets . . . . small, bright dark orange: ray—few, ...") supplemented by the authentic *Colenso* specimen at Kew. This has the one flowering head now lacking rays, but the aspect of the various critical structures is more properly that of the variety *minor* than of *B. pilosa* proper.

EXPLANATION OF PLATES XIX–XXII

PLATE XIX

Coreopsis ochracea; a, b, flowering branch and foliage, ×0.63; *c, d*, exterior involucral bracts, ×2.5; *e*, interior involucral bract, ×2.5; *f*, ligulate floret, ×1.9; *g*, palea, ×2.5; *h*, disc floret, ×2.5; *i*, immature achene, ×4; all from *W. Goetze* 731, type, in Herb. Berl.

PLATE XX

Bidens pilosa var. *calcicola: a*, flowering and fruiting specimen, ×0.64; *b*, exterior involucral bract, ×4.5; *c*, interior involucral bract, ×4.5; *d*, ligulate floret, ×4.5; *e*, palea, ×4.5; *f*, disc floret, ×4.5; *g*, outer and *h*, inner achenes, ×4.5; *a* from *Kerber*, Cordoba, Vera Cruz, Mexico, July 22, 1882, in Herb. Berl.; *b–h*, from *Berlandier* 5 and 113, cotypes in Herb. Par.

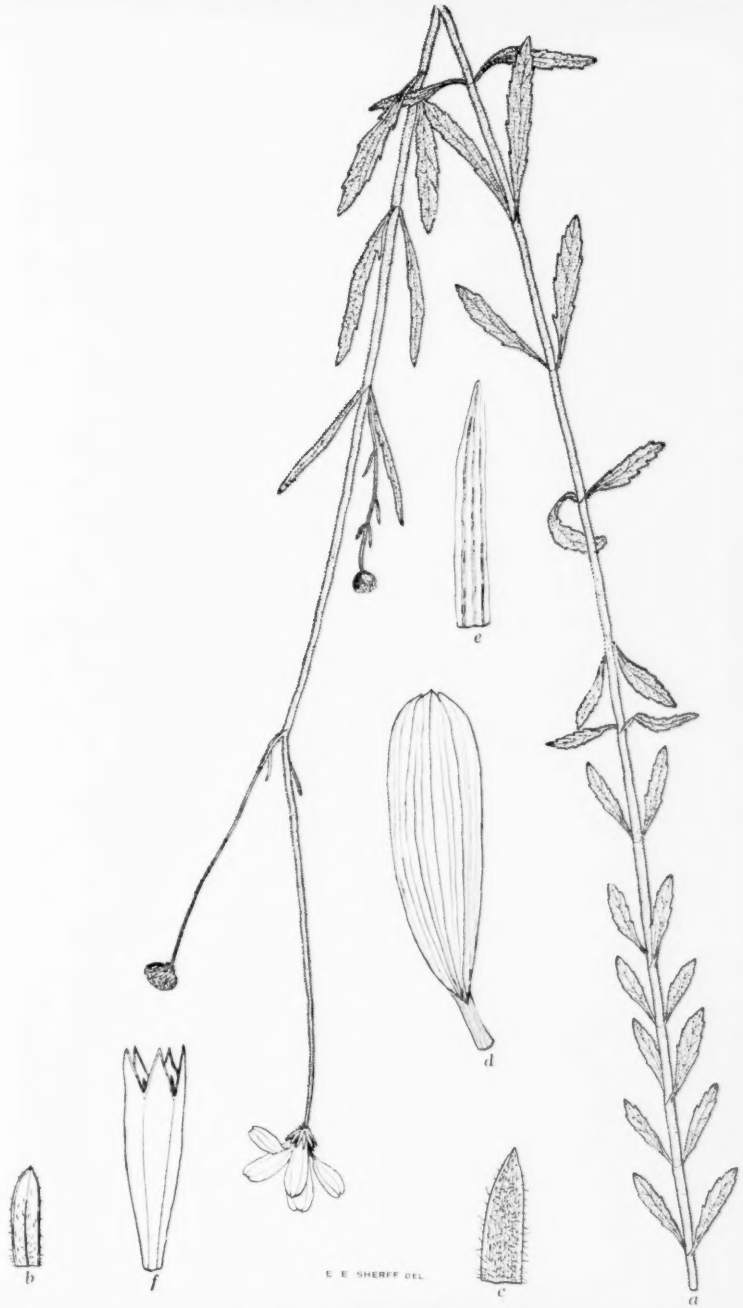
[21] *Cf.* O. E. SCHULZ (Engler Bot. Jahrb. **50** [Suppl.] 179. 1914), " . . . . dagegen gehoren *B. sundaicus* . . . . und var. *minor* . . . . wahrscheinlich zu *B. pilosus* L. var. *dubius* (Cass.) O. E. S."

[22] My manuscript lists more than 150 collections, but many others had been omitted for lack of space.

[23] In my own cultural observations, the var. *minor* appeared to come very true to a given type. Thus, for example, in some two dozen plants (*Sherff* 2043, Herb. Field Mus., etc.), raised in 1915 from achenes on specimens sent me by M. ST. AHNNE (Bot. Gard. Raoul, Papeete, Isl. Tahiti), the hundreds of flowering heads had uniformly tiny, distinctly yellowish ligulate florets, as had been observed on the parent material.

SHERFF on COMPOSITAE

SHERFF on COMPOSITAE



SHERFF on COMPOSITAE

SHERFF on COMPOSITAE

PLATE XXI

Bidens triplinervia (atypic, the form described for *B. hirtella*): *a*, flowering branch, ×0.72; *b*, exterior involucral bract, ×0.86; *c*, interior involucral bract, ×0.86; *d*, ligule, ×2.9; *e*, palea, ×0.86; *f*, corolla of disc floret, ×0.86; all from Humboldt and Bonpland, type of *B. hirtella*, in Herb. Par.

PLATE XXII

Bidens triplinervia var. *mollis:* *a*, *b*, flowering and foliage branches, ×0.73; *c*, portion of leaf, ×2.9; *d*, exterior involucral bract, ×4.4; *e*, interior involucral bract, ×4.4; *f*, ligule, ×2.2; *g*, palea, ×4.4; *h*, corolla of disc floret, ×4.4; *i*, achene, ×4.4; *a*, *b*, from *R. Spruce* 5047, at foot of Mt. Tunguragua, Ecuador, Herb. Mus. Vienna; *c–h* from *E. Poeppig* 1377, type, in Herb. Mus. Vienna; *B. triplinervia* var. *macrantha*, atypic, the form described for *B. attenuata*): *j*, stem leaf, ×1.46 (seen from beneath, leaves mostly flattened out but petiole left convolute, its ciliation thus not showing) *k*, exterior involucral bract, ×4.4; *l*, interior involucral bract, ×4.4; *m*, ligule, ×2.2; *n*, palea, ×4.4; *o*, corolla of disc floret, ×4.4; *p*, achene, ×4.4; *j–p* from *Ghiesbreght* 85 *pro parte*, Chiapas, Mexico, type in Herb. Gray.

EFFECTS OF LIME AND POTASH FERTILIZERS ON CERTAIN MUCK SOILS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY **342**

WALTER FERDINAND LOEHWING

(WITH SEVEN FIGURES)

Introduction

Ordinary methods of fertilizer practice have repeatedly been found poorly adapted to muck soils. Applications of mineral nutrients, apparently deficient in these organic soils, have frequently proved injurious instead of beneficial to crops in the field. Injurious results from applications of lime and potash have been reported for mucks exhibiting positive acidity and chemical deficiency of potassium. Results of experiments on such soils are mentioned more specifically later. In this report analyses of plants grown on such muck soils are presented for comparison with those of plants grown on soils showing favorable responses to lime and potash applications, in order to disclose the difference in the balance of nutrients within the tissues which accompany injury from fertilizers.

The term muck is here employed to designate dark colored or black soils high in organic matter, light in weight, and pulverulent or downy in texture. Mucks are distinguished from peats by their greater weight and decomposition of vegetable detritus, plant structures being unrecognizable. Mucks often resemble fertile humus soils in color and texture, but differ widely from them in organic content, temperature, and water retentivity. Ability to cultivate peats and mucks would add millions of acres to the world's most valuable farm lands, since these soils lie predominantly in the grain belts. DACHNOWSKI (**6**) estimates that Europe has 77 million, Canada 30 million, and the United States 20 million acres of unproductive peats and mucks. The works of SOPER (**25**), DACHNOWSKI, BERSCH (**3**), SEELHORST (**24**), and PUCHNER (**21**) review the enormous literature on this subject, and bring up to date the existing information on agricultural practices adapted to these soils.

Fertilizer tests showing injurious effects of lime on corn in swamp lands of Kankakee, Mason, and Tazewell Counties, Illinois, have been reported by HOPKINS, READHIMER, AND FISHER (12). These were four year field experiments in which the effects of limestone were consistently injurious to corn. GAMBLE and SLATER (10) reported a five year field test in which the effects of lime and potassium on oats proved beneficial when applied separately, but injurious when combined. Fertilizer tests on muck soils of Indiana reported by CONNER and ABBOTT (5) show some soils which do not respond favorably to any ordinary treatment. CONNER also reported a muck from Newton County, Indiana, showing a lime requirement of 20,000 parts per million which was not benefited by lime applications. European investigators have also reported diminution in crop yields following fertilizer applications on muck soils. Thus EHRENBERG (8, 9), ARND (1), and DUMONT and CROCHETELLE (7) have pointed out that lime and potash fertilizers may often prove deleterious, even though soil analyses reveal apparent deficiencies in these elements. The mucks studied by these investigators, as well as those discussed in this report, do not include "alkali" or "bogus" soils excessively high in soluble salts, iron, or aluminum. CONNER (4) shows that unproductive black soils containing excess soluble salts differ in numerous ways from true mucks.

Experimental procedure

Mucks known to show a decided response to lime and potash in the field were collected at various localities and shipped to the University of Chicago. Seven pounds of each soil were placed in glazed, one gallon earthenware pots, and treated with mineral fertilizers as indicated later. Each series was set up in duplicate for purposes of comparison and to insure ample material for analysis. Tests were conducted in a greenhouse with the temperature maintained between 18° and 27° C. After planting, water was added to soils until the weight of pot contents was 8.5 pounds, the water representing approximately 20 per cent of the soil weight. This apparently optimum moisture content was readily maintained throughout the experiments, as evaporation in the greenhouse was only moderate. Four different crop plants were tested, including Marquis Hard

wheat, Yellow Dent corn, Victory oats, and Mammouth Red Fancy clover. Wheat, oats, and clover were thinned to fifteen and corn to five plants per pot at the end of the second week. Each crop was grown on four muck soils which differed in their responses to potash and lime amendments. At the end of the tenth week, pot contents were removed *in totem* to a pan, roots washed free of soil, rinsed in distilled water, and dried on filter paper. The entire crop from each pot was then weighed and hashed in a Nixtamel mill. After thorough mixing, samples were taken for moisture determinations, and the remaining green hash pickled for storage in 80 per cent boiling alcohol containing 2 gm. chemically pure calcium carbonate per liter.

TABLE I

ANALYSES OF UNTREATED MUCK SOILS

	Soil 1 percentage	Soil 2 percentage	Soil 3 percentage	Soil 4 percentage
Hygroscopic moisture	8.20	12.21	3.43	15.30
Total potassium	0.29	1.52	0.30	1.05
Total calcium	3.44	0.08	1.67	3.54
Total magnesium	0.40	0.10	0.18	1.02
Total iron	1.21	2.02	0.10	2.22
Total phosphorus	0.19	0.08	0.34	0.20
Total sulphur	0.54	0.11	0.44	0.20
Total nitrogen	3.62	1.42	3.90	1.22
Total volatile matter	48.10	42.61	83.00	47.78
Insoluble silicates, etc.	15.50	26.80	5.10	24.40
Lime requirements in ppm	2700.00	3500.00	2700.00	1200.00

Alcohol was evaporated at the beginning of analyses, materials transferred to glass stoppered weighing bottles, and dried to constant weight in a vacuum oven at 80° C. Four soils were employed in the experiment, as follows:

1. Black powdery acid muck from Manito, Mason County, Illinois. This soil showed injury to cereals when lime was added to correct acidity. It responded favorably to potash.

2. Sandy acid muck from Mill Creek, between Mud and Fish Lakes, La Porte County, Indiana. Crops on this soil were injured by lime and by potash.

3. Light weight acid muck from Newland, Jasper County, Indiana, known to respond favorably to lime but unfavorably to potash.

4. Black acid muck from farm of Mr. PETER LARSEN, near

Hopkins, Minnesota, known to respond very favorably to lime and potash fertilizers. Analyses of these soils are given in table I.

Pots of each soil were treated with powdered, chemically pure salts as follows: Pot A (control): untreated soil; Pot B: 400 ppm

TABLE II

ANALYSES OF YELLOW DENT CORN GROWN ON FOUR MUCK SOILS

FERTILIZER ADDED (PPM)	PLANT WEIGHT (GM.)	PERCENTAGE						
		MOISTURE	POTASSIUM	CALCIUM	ORGANIC NITROGEN	NITRATE NITROGEN	TOTAL SUGARS	CARBOHYDRATE
	Soil 1							
None (check)	7.45	82.4	0.42	0.18	1.91	0.14	5.02	9.12
400 KCl	8.50	79.8	0.78	0.14	2.05	0.04	7.12	11.13
4000 $CaCO_3$	6.20	82.7	0.30	0.21	1.65	0.09	4.54	8.04
4000 $CaCO_3$ 400 KCl	7.10	81.7	0.74	0.22	1.74	0.20	4.87	8.98
8000 $CaCO_3$ 400 KCl	7.15	82.4	0.60	0.22	1.70	0.10	4.66	8.01
	Soil 2							
None (check)	6.88	81.4	0.45	0.15	1.82	0.12	6.20	10.11
400 KCl	4.75	82.8	0.62	0.14	1.75	0.18	4.40	9.10
4000 $CaCO_3$	5.95	82.1	0.12	0.23	1.54	0.35	6.09	8.42
4000 $CaCO_3$ 400 KCl	5.20	80.9	0.43	0.23	1.50	0.28	6.17	8.98
8000 $CaCO_3$ 400 KCl	5.40	80.7	0.44	0.23	1.71	0.09	5.85	8.90
	Soil 3							
None (check)	8.40	82.7	0.62	0.13	1.85	0.08	3.67	10.59
400 KCl	8.00	81.7	0.65	0.10	1.80	0.40	5.36	9.67
4000 $CaCO_3$	5.80	81.0	0.58	0.20	1.58	0.28	3.81	8.28
4000 $CaCO_3$ 400 KCl	7.20	83.4	0.59	0.21	1.58	0.31	3.70	9.50
8000 $CaCO_3$ 400 KCl	7.05	83.6	0.59	0.29	1.82	0.11	3.70	9.59
	Soil 4							
None (check)	4.45	81.1	0.61	0.11	1.81	0.36	5.11	8.41
400 KCl	6.28	79.5	0.77	0.10	2.00	0.15	5.25	8.87
4000 $CaCO_3$	6.25	80.4	0.60	0.24	1.78	0.20	4.87	8.00
4000 $CaCO_3$ 400 KCl	7.70	80.6	0.78	0.24	2.01	0.07	5.38	8.40
8000 $CaCO_3$ 400 KCl	7.00	80.1	0.79	0.24	2.01	0.07	5.19	8.79

potassium chloride; Pot C: 4000 ppm calcium carbonate; Pot D: 4000 ppm calcium carbonate and 400 ppm potassium chloride; Pot E: 8000 ppm calcium carbonate and 400 ppm potassium chloride.

The minerals were sifted into and thoroughly mixed with the soil. Series were run in duplicate. A third series, in which calcium acid phosphate was added throughout at the rate of 400 ppm, showed that plants on these soils did not respond to phosphorus. Etiolation

effects indicative of phosphorus shortage were not noticed on any untreated soil employed in the experiments.

Analytical methods

Soil analyses were made by the methods of the Association of Official Agricultural Chemists (2), potassium being determined as

TABLE III

ANALYSES OF MARQUIS HARD WHEAT GROWN ON FOUR MUCK SOILS

FERTILIZER ADDED (PPM)	PLANT WEIGHT (GM.)	PERCENTAGE						
		MOISTURE	POTASSIUM	CALCIUM	ORGANIC NITROGEN	NITRATE NITROGEN	TOTAL SUGARS	CARBOHYDRATE
		Soil 1						
None (check)	4.74	86.4	0.55	0.21	0.88	0.03	6.35	10.24
400 KCl	5.80	88.5	0.78	0.17	0.90	0.01	5.77	12.75
4000 $CaCO_3$	2.70	89.0	0.49	0.28	0.80	0.73	3.72	9.14
4000 $CaCO_3$ 400 KCl	3.55	85.2	0.62	0.10	1.14	0.10	4.23	9.01
8000 $CaCO_3$ 400 KCl	3.20	88.1	0.51	0.27	0.89	0.51	3.70	9.24
		Soil 2						
None (check)	4.64	84.2	0.61	0.22	0.92	0.72	4.77	11.45
400 KCl	2.30	86.4	0.77	0.18	0.78	0.42	3.32	8.07
4000 $CaCO_3$	3.81	85.3	0.57	0.41	0.92	0.76	4.25	9.44
4000 $CaCO_3$ 400 KCl	3.28	87.0	0.65	0.20	0.92	0.26	4.00	9.66
8000 $CaCO_3$ 400 KCl	2.95	87.7	0.50	0.44	0.87	0.91	4.29	9.54
		Soil 3						
None (check)	5.52	82.2	0.31	0.31	1.71	0.00	5.21	10.70
400 KCl	4.32	85.4	0.61	0.19	1.22	0.59	5.46	8.92
4000 $CaCO_3$	2.66	82.7	0.21	0.42	0.68	0.82	3.21	9.70
4000 $CaCO_3$ 400 KCl	3.15	83.9	0.25	0.34	0.90	0.78	5.20	8.42
8000 $CaCO_3$ 400 KCl	2.98	82.3	0.24	0.34	0.78	0.69	4.94	8.66
		Soil 4						
None (check)	3.97	83.0	0.61	0.18	0.73	0.69	3.92	9.02
400 KCl	3.82	84.6	0.70	0.10	0.97	0.47	4.83	10.19
4000 $CaCO_3$	4.47	82.7	0.44	0.31	0.99	0.71	5.22	10.80
4000 $CaCO_3$ 400 KCl	4.93	82.3	0.76	0.34	1.03	0.74	5.61	10.52
8000 $CaCO_3$ 400 KCl	4.28	81.8	0.60	0.33	0.82	0.41	4.44	9.45

its chloroplatinate, and calcium titrated as oxalate against potassium permanganate. Lime requirement in parts per million was determined by the Veitch method (15).

Entire plants including roots were analyzed. Moisture content is expressed as percentage of wet weight. Potassium, calcium, and

phosphorus were determined by sulphuric acid combustion methods. The oxidized residues were transferred to platinum crucibles, and the sulphuric acid carefully evaporated on hot plates, followed by ignition to drive off ammonia for calcium and potassium determinations. Calcium was precipitated as oxalate, and potassium as its

TABLE IV

ANALYSES OF VICTORY OATS GROWN ON FOUR MUCK SOILS

FERTILIZER ADDED (PPM)	PLANT WEIGHT (GM.)	PERCENTAGE						
		MOISTURE	POTASSIUM	CALCIUM	ORGANIC NITROGEN	NITRATE NITROGEN	TOTAL SUGARS	CARBOHYDRATE
		Soil 1						
None (check)	4.38	81.1	1.01	0.17	1.81	0.20	3.83	8.45
400 KCl	4.87	82.3	1.23	0.22	2.02	0.02	4.02	9.05
4000 $CaCO_3$	2.76	87.0	0.99	0.25	1.80	0.80	4.11	7.60
4000 $CaCO_3$ 400 KCl	4.05	84.7	1.23	0.23	2.07	0.35	3.95	8.24
8000 $CaCO_3$ 400 KCl	3.16	80.9	1.00	0.25	1.98	0.58	4.71	7.78
		Soil 2						
None (check)	4.24	81.5	0.77	0.15	1.40	0.31	4.46	8.97
400 KCl	2.10	80.5	0.97	0.09	1.98	0.06	5.02	7.80
4000 $CaCO_3$	4.70	83.1	0.49	0.20	0.88	0.87	4.88	7.77
4000 $CaCO_3$ 400 KCl	2.98	82.7	0.75	0.16	1.18	0.02	5.41	8.37
8000 $CaCO_3$ 400 KCl	2.46	82.4	0.48	0.20	1.07	0.84	5.00	7.60
		Soil 3						
None (check)	3.46	84.3	0.44	0.28	1.74	0.14	3.34	10.64
400 KCl	3.12	81.3	0.64	0.20	1.40	0.20	3.74	9.92
4000 $CaCO_3$	2.50	82.0	0.32	0.40	1.01	0.56	3.20	9.25
4000 $CaCO_3$ 400 KCl	2.69	84.6	0.36	0.39	1.23	0.21	3.82	9.75
8000 $CaCO_3$ 400 KCl	2.39	82.4	0.31	0.39	1.02	0.24	3.71	9.03
		Soil 4						
None (check)	3.11	83.2	0.68	0.18	1.63	0.59	4.47	8.99
400 KCl	3.70	86.2	0.78	0.14	1.82	0.49	5.26	9.42
4000 $CaCO_3$	3.24	83.4	0.65	0.19	1.84	0.36	5.42	9.32
4000 $CaCO_3$ 400 KCl	3.82	84.5	0.76	0.21	1.88	0.26	5.56	9.84
8000 $CaCO_3$ 400 KCl	3.01	82.5	0.74	0.19	1.63	0.22	5.31	9.79

cobaltinitrite. Each was titrated against standard potassium permanganate. Phosphorus was determined as ammonium phosphomolybdate by the Neumann-Pemberton (2) method, but is not reported because its variations (between 0.15 and 0.38 per cent) were small and apparently of no significance. Nitrogen was determined by the Gunning method (2). Tables II–V show as organic nitrogen

the percentage of nitrogen obtained without the use of salicylic acid in the digestion mixture. Nitrate nitrogen represents the increase over organic nitrogen in nitrogen content found when digestion was performed with a one to thirty salicylic-sulphuric acid

TABLE V

ANALYSES OF MAMMOTH RED FANCY CLOVER GROWN ON FOUR MUCK SOILS

FERTILIZER ADDED (PPM)	PLANT WEIGHT (GM.)	PERCENTAGE						
		MOISTURE	POTASSIUM	CALCIUM	ORGANIC NITROGEN	NITRATE NITROGEN	TOTAL SUGARS	CARBOHYDRATE
	Soil 1							
None (check)	2.00	81.7	0.71	0.22	2.31	0.26	4.81	10.42
400 KCl	1.72	83.5	0.98	0.18	1.75	0.43	4.00	10.07
4000 $CaCO_3$	2.41	80.9	0.70	0.28	2.49	0.03	5.41	11.44
4000 $CaCO_3$ 400 KCl	2.16	80.8	0.84	0.26	1.98	0.34	4.08	10.06
8000 $CaCO_3$ 400 KCl	2.39	80.5	0.85	0.28	2.00	0.11	3.85	8.97
	Soil 2							
None (check)	1.95	82.7	0.80	0.19	2.42	0.01	5.27	8.90
400 KCl	1.46	83.2	0.99	0.17	1.82	0.60	4.81	7.05
4000 $CaCO_3$	2.18	82.8	0.75	0.23	1.70	0.41	5.44	7.81
4000 $CaCO_3$ 400 KCl	1.74	82.0	0.64	0.23	1.48	0.62	5.77	7.57
8000 $CaCO_3$ 400 KCl	1.90	82.2	0.69	0.24	1.48	0.61	3.24	6.71
	Soil 3							
None (check)	2.41	80.7	0.41	0.11	1.31	0.04	4.42	8.50
400 KCl	1.72	81.6	0.67	0.10	1.44	0.08	4.47	8.67
4000 $CaCO_3$	2.26	81.6	0.69	0.16	1.50	0.11	5.21	10.77
4000 $CaCO_3$ 400 KCl	2.18	81.5	0.68	0.15	1.57	0.04	3.92	9.09
8000 $CaCO_3$ 400 KCl	2.40	81.6	0.69	0.15	1.54	0.08	3.41	9.41
	Soil 4							
None (check)	1.78	82.4	0.55	0.15	2.16	0.37	3.58	8.78
400 KCl	1.25	81.5	0.84	0.16	2.54	0.14	5.41	10.12
4000 $CaCO_3$	2.27	82.0	0.42	0.22	2.71	0.10	6.35	10.42
4000 $CaCO_3$ 400 KCl	2.04	81.7	0.90	0.28	2.70	0.07	5.08	10.48
8000 $CaCO_3$ 400 KCl	1.62	81.3	0.52	0.26	2.25	0.30	4.82	10.00

mixture. The quantities of nitrate nitrogen in these young plants appeared great enough to justify determination.

Total sugars were determined in the F_1 and F_2 (water-alcohol-ether soluble) fractions of the tissue extracts by the Bertrand volumetric method. Copper values are expressed in glucose equivalents as given in the Munson-Walker tables (**2**). Percentages are ex-

pressed on the basis of total dry weight of the sample (F_1 plus F_2 plus F_3).

Total carbohydrates include the carbohydrates, calculated as starch, in the insoluble F_3 fraction hydrolyzed by strong hydrochloric acid, plus the total soluble sugars of the F_1 and F_2 fractions.

Discussion

The data confirm the oft proved and well known fact that it is impossible to determine the fertilizer needs of soils from their chemical analyses. Soil 1, high in calcium and low in potassium, responded

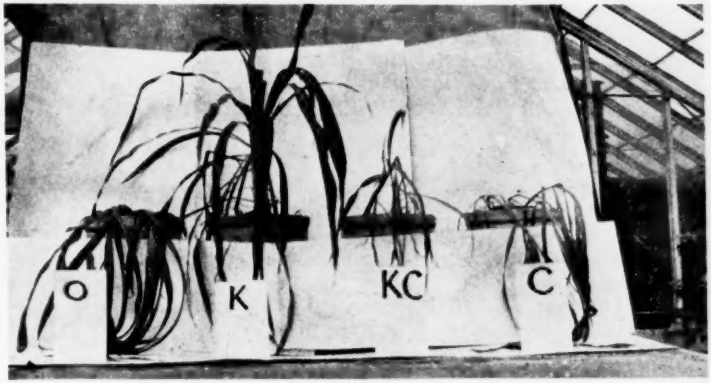


FIG. 1.—Injurious effect of calcium carbonate on Soil 1: *O*, check; *K*, 400 ppm KCl; *KC*, 400 ppm KCl plus 4000 ppm $CaCO_3$; *C*, 4000 ppm $CaCO_3$.

favorably to potash but unfavorably to lime, as shown in fig. 1. Soil 2, high in potash but low in lime, responded unfavorably to both fertilizers (fig. 2). Soil 3, high in potash and medium in lime, was injured by potassium (fig. 3), while Soil 4. high in both, responded favorably to both, as shown in fig. 4. The injurious effects of lime are astonishing in view of the known acidity of these soils, and must consequently be explained by the action of lime on soil nutrients, the net result of which is unfavorable to crops. ROBINSON (**23**), working on Michigan mucks, found that liming frequently was injurious, in some cases entirely offsetting the benefit of potassium fertilizers. NOLTE (**17**) points out that alkali salts increase soil density and capillary water capacity, making them physiologically

dry, a conclusion confirmed by EHRENBERG (9), who also has found that too much lime may depress potassium assimilation. The importance of the physiological availability of potassium and calcium salts is shown by the fact that their concentration in tissues

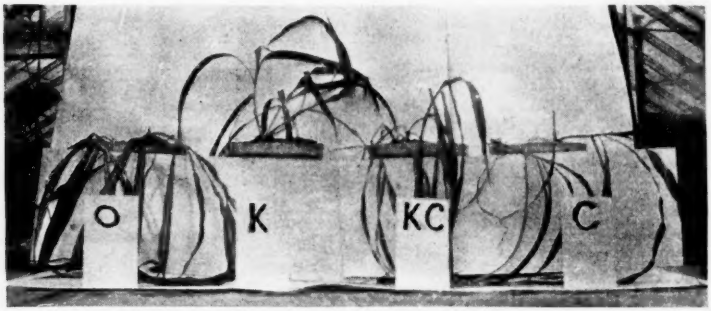


FIG. 2.—Injurious effect of potassium chloride and calcium carbonate on Soil 2: *O*, check; *K*, 400 ppm KCl; *KC*, 400 ppm KCl plus 4000 ppm $CaCO_3$; *C*, 4000 ppm $CaCO_3$.

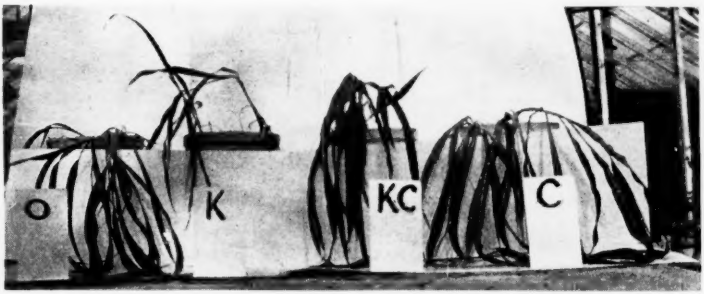


FIG. 3.—Injurious effect of potassium chloride on Soil 3: *O*, check; *K*, 300 ppm KCl; *KC*, 400 ppm KCl plus 4000 ppm $CaCO_3$; *C*, 4000 ppm $CaCO_3$.

varies independently of the concentration of these bases in the soils.

Ordinary experimental methods for determination of availability of plant foods in soils are not adapted to mucks. It was found extremely difficult to avoid the adsorptive effects of organic colloids. Soil extracts, initially acid to indicators, may turn alkaline on stand-

ing. Colloid phenomena such as these were accompanied by great variations in concentration of plant nutrients, especially potassium and calcium. PUCHNER (**22**) reported similar observations on extracts of humus soils in Europe. Humus colloids form complexes with calcium, iron, and magnesium which are soluble in excess ammonia, as has been pointed out by OSTWALD (**18**). The selection of fertilizers on the basis of soil extracts has proved insecure for mineral soils, and is less secure for mucks. The accompanying tissue

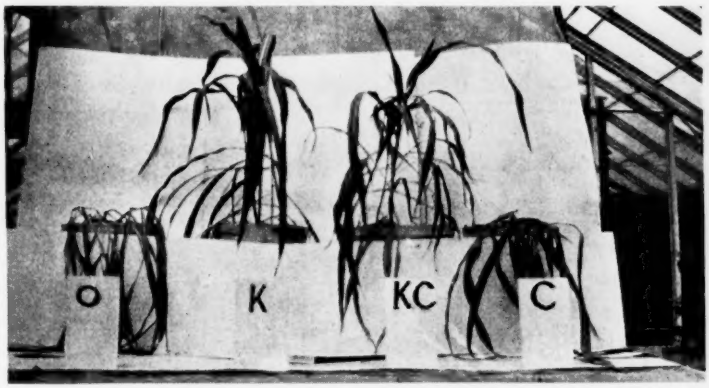


FIG. 4.—Influence of potassium fertilizer in increasing stem erectness of corn: *O*, check; *K*, 400 ppm KCl; *KC*, 400 ppm KCl plus 4000 ppm $CaCO_3$; *C*, 4000 ppm $CaCO_3$ on Soil 4.

analyses reveal some of the changes in nutrients within the plants following applications of lime and potash.

One of the most striking results shown by the experiments is the effect of potash fertilizers. Cereals treated with potash were much more erect than those untreated; the latter were decumbent and sprawling (fig. 4). KRAUS (**13**) and WALSTER (**27**) observed similar results in other crops in the absence of potassium.

The concentration of potassium and calcium increased in tissues when these salts were used as fertilizers, thus indicating increased availability in spite of the tendency of the humus colloids to adsorb mineral bases. The effect of potash on stem erectness is especially striking in view of the fact that increase in potassium induces a

depression in calcium content of cereals (tables II–IV). Abundance of calcium alone did not seem sufficient for production of sturdy, erect plants, since limed pots with soils low in potash usually contained sprawling or lopped-over crops. Depression of calcium content by potassium was found generally to be the case except in clover (table V).

Calcium likewise diminished the potash content of tissues in all cases, including clover, showing the balance between lime and potash to be a very delicate one. These observations coincide with those of EHRENBERG (**9**), who used lime and potash fertilizers for wheat and barley grown in sand cultures. From his own results and the data of many other workers, which are reviewed by him, EHRENBERG derived his well known lime-potash law. He states that, when lime intake is greatly increased in plants poorly supplied with potassium, absorption of the latter is diminished, often making its absence a limiting factor in development. EHRENBERG's analyses do not give calcium, thus leaving the effect of potassium on calcium content of tissues in his experiments unknown. By the use of data given in tables II–V, it is possible to express the effects of potassium and calcium fertilizers on the calcium and potassium content of tissues as a ratio of one to the other, the value of this ratio, K/Ca in the tissues, being diminished by lime but increased by potash fertilizers. These changes are usually caused by an actual depression of one element and a positive increase of the other in plants. In clover the best crop yields were uniformly associated with a low K/Ca ratio; this was not the case in cereals. From these facts it appears that the value of the K/Ca ratio is more significant in connection with crop production of clover than of cereals. This may hold true for the legumes generally. The better grain crops were characterized by relatively high potassium and nitrogen content, rather than by any particular value of the K/Ca ratio.

From the data in table VI it is apparent that potash uncombined with lime may prove undesirable as a muck fertilizer for clover. VANDECAVEYE (**26**), working with potassium fertilizers, found them beneficial to wheat but not to clover. Only on Soil 4 did potash seem beneficial for clover, and even in this case not beneficial per se, but rather because potash assisted in increasing the calcium content

of the tissues. As there were no marked differences in root systems of the cultures, it appears that the injurious action of potassium on clover is due to disturbance of normal carbohydrate and protein synthesis. Dry weight, soluble sugars, total carbohydrates, and organic nitrogen of clover increased with rise in calcium content but diminished with increase in K/Ca ratio. These nutrient relations did not occur uniformly in cereal crops, and possibly they may represent distinctive differences between leguminous and non-leguminous types of plants.

Injurious effects of a given fertilizer seem to predominate when it

TABLE VI

RELATION OF K/CA RATIO TO CROP YIELD IN CLOVER

SOIL NO.	TREATMENT (PPM)	AVERAGE WEIGHT (GM.) PER PLANT	POTASSIUM PERCENTAGE	CALCIUM PERCENTAGE	K/Ca RATIO
1B	400 KCl	1.72	0.98	0.18	5.4
1C	4000 $CaCO_3$	2.41	0.70	0.28	2.6
2B	400 KCl	1.46	0.99	0.17	5.8
2C	4000 $CaCO_3$	2.18	0.75	0.23	3.2
3B	400 KCl	1.72	0.67	0.10	6.7
3C	4000 $CaCO_3$	2.46	0.69	0.16	4.3
4B	400 KCl	1.25	0.84	0.16	5.3
4C	4000 $CaCO_3$	2.27	0.42	.022	1.5

is applied in a mixture with another known to be beneficial. Injury is marked externally by retardation of growth, etiolation and lopping-over of plants. On Soil 1, showing injury to grains following lime applications, the injurious effect of lime predominated when both lime and potash were applied, although potash alone induced a favorable response on this soil, as shown in fig. 1. This behavior is similar to one reported by ROBINSON (**23**), working with beets on mucks in Michigan. According to EHRENBERG'S (**9**) interpretation of the action of lime, addition of potassium should have offset injury due to lime. The fact that this was not the case may be due to the high absorptive capacity of mucks. On Soil 3 lime singly was beneficial, but potassium chloride singly proved injurious, its injurious effect prevailing when it and calcium carbonate were ap-

plied together. It is questionable, of course, whether the injury here was due to potassium or chloride ions, as mucks may adsorb potassium, leaving harmful chlorides in the soil. Such preferential adsorption may explain the responses on Soil 3 and on Soil 2, for which neither lime nor potash proved beneficial. In short, in the experiments here reported, the effects of the injurious fertilizer of a combination seemed to predominate over those of the beneficial

TABLE VII

EFFECTS OF INJURIOUS FERTILIZERS ON NITROGEN AND CARBOHYDRATE CONTENT OF TISSUES

SOIL NO.	TREATMENT (PPM)	CROP	WEIGHT PER PLANT IN GRAMS	INJURED BY	ORGANIC NITROGEN PERCENTAGE	TOTAL CARBOHYDRATES PERCENTAGE
1A	None (check)	Corn	8.24		1.91	9.12
1C	4000 $CaCO_3$	Corn	6.20	Ca	1.65	8.04
3A	None (check)	Corn	8.40		1.85	10.59
3B	400 KCl	Corn	8.00	K	1.80	9.67
1A	None (check)	Wheat	4.74		0.88	10.24
1C	4000 $CaCO_3$	Wheat	2.70	Ca	0.80	9.14
3A	None (check)	Wheat	5.52		1.71	10.70
3B	400 KCl	Wheat	4.32	K	1.22	8.92
1A	None (check)	Oats	4.38		1.81	8.45
1C	4000 $CaCO_3$	Oats	2.76	Ca	1.80	7.60
3A	None (check)	Oats	3.46		1.74	10.64
3B	400 KCl	Oats	3.12	K	1.40	9.92
1A	None (check)	Clover	2.00		2.31	10.42
1B	400 KCl	Clover	1.72	K	1.75	10.07
2A	None (check)	Clover	1.95		2.42	8.90
2B	400 KCl	Clover	1.46	K	1.82	7.05

much as though the latter fertilizer were not present. These results point to an absence of ionic antagonism, as reported by LOEW (**14**), GERICKE (**11**), and others, in which one ion entirely counteracted the deleterious effects of another. Injury from fertilizers is characterized internally by a depression of the organic nitrogen and total carbohydrate content of the tissues, as shown in table VII and fig. 5.

High calcium tissues of the cereals contained a relatively high amount of nitrate nitrogen, as shown in fig. 6 and table VIII. This may be due to the fact that lime increases soil nitrates, as has been reported by PIPER (**19**) and other investigators. Conversely, plants having a high K/Ca ratio contained relatively smaller amounts of

nitrate nitrogen but more organic nitrogen, as shown in fig. 7, indicating that potassium may function in the synthesis of proteins as well as carbohydrates. Since high calcium signifies also low potassium content, it might be concluded that the plant cannot synthesize the abundant soluble nitrogen without the presence of more potassium.

The ratio of nitrogen to potassium, N/K in the tissues, shows the

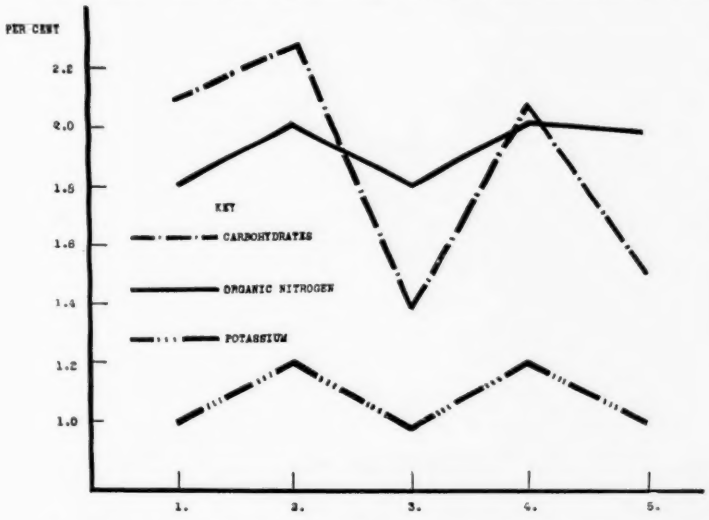


FIG. 5.—Relation of potassium to carbohydrate and organic nitrogen content of oat tissues (data from table IV, Soil I); carbohydrate percentages have been divided by 4.

balance between this fertilizer and protein synthesis, since organic nitrogen is a direct index to protein content of tissues. This N/K ratio is widened by lime primarily because the latter greatly diminishes the potassium content of plant tissues. Where this depression is too great, lack of potassium may become a limiting factor in carbohydrate and protein synthesis, resulting finally in cessation of plant growth. Lack of potassium would certainly have this effect if protein synthesis within the plant occurs in the manner that the work of PRIANISCHNIKOW (**20**) seems to indicate. He finds that proteins are formed from inorganic nitrogen only in the presence of

carbohydrates. He considers the stages in protein synthesis as follows: Carbohydrates+inorganic nitrogen⇌acid amides⇌amino acids⇌proteins. In the absence of carbohydrates, he finds that this process reverses, giving an accumulation of inorganic nitrogen in the plant. If potassium is essential for carbohydrate synthesis, another step is merely added to the process. It has long been known that potassium starvation interferes with carbohydrate storage,

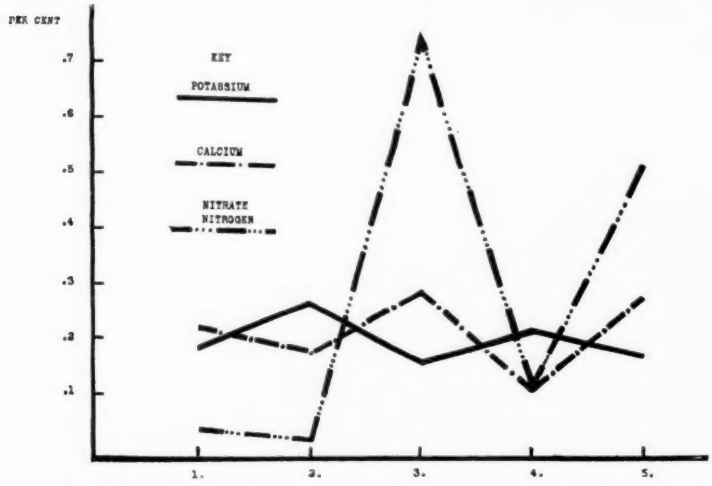


FIG. 6.—Relation of calcium and potassium to nitrate nitrogen in wheat tissues (data from table III, Soil I); potassium percentages have been divided by 3.

either by inhibiting synthesis or translocation of sugars. Carbon dioxide plus water plus potassium→carbohydrates, which, in the presence of inorganic nitrogen, lead to protein formation, as already indicated. Proteins and carbohydrates are largely substituted hydrocarbon chains in which the synthetic mechanism may not unlikely be similar, the end result depending upon the radicals replacing the original hydroxyl groups.

The analytical data reveal the fact that it is not possible to correlate crop production with either the potassium-calcium ratio or the carbohydrate-nitrogen ratio of cereal tissues, as high and low ratios among good and poor crops are almost equally common. This

may be true only in tissues of essentially young plants, such as were analyzed in this case. Mature tissues probably exhibit quite different relations, especially in connection with soluble constituents. Whether nutrient ratios in mature cereals grown on muck soils would afford an index to the character of crops remains a matter for future determination. Soluble sugars and nitrate nitrogen did not vary uniformly with insoluble carbohydrates or organic nitrogen of tissues. High yield and quality of crops seems to be correlated with high organic nitrogen and high total carbohydrates.

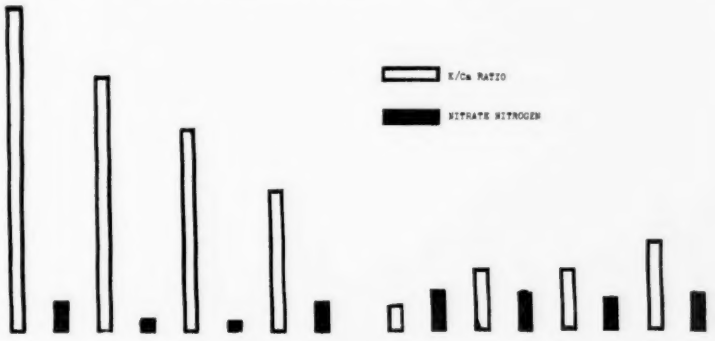


FIG. 7.—Relation of K/Ca ratio to nitrate nitrogen content of wheat tissues grown on four different soils; nitrate nitrogen content varies inversely with value of K/Ca ratio (cf. fig. 6); data from table VIII.

The relation between chemical and physical factors involved in crop production seems to be more complex on muck than on mineral soils, due largely to the greater amount of colloidal organic material in the former. As these highly colloidal soils have a great adsorption capacity, they may on one hand conserve nutrient elements by prevention of leaching, but on the other hand create a physiological deficiency of nutrients by withholding them from plants. Since bases are to some extent replaceable, the effect of a basic fertilizer on mucks might depend largely on the influence of other ions liberated by it, as well as on its own direct action. In colloids highly laden with potassium, injury to crops after heavy liming may be due to liberation of alkali carbonates and their toxic or plasmolytic effects. It is possible that lime used to correct acidity liberates such

alkalis not only by replacement, but also by its coagulative action, lime being known to coagulate colloids and reduce indices of swelling in soils (**18**). Alkali carbonates so liberated may prove more objec-

TABLE VIII

RELATION OF NITRATE NITROGEN TO CALCIUM AND POTASSIUM CONTENT OF TISSUES OF CORN, WHEAT, AND OATS

SOIL NO.	TREATMENT (PPM)	CROP	AVERAGE WEIGHT PER PLANT (GM.)	POTASSIUM PERCENTAGE	CALCIUM PERCENTAGE	K/Ca RATIO	NITRATE NITROGEN PERCENTAGE
1B.....	400 KCl	Corn	8.50	0.78	0.14	4.8	0.04
1C.....	4000 $CaCO_3$	Corn	6.20	0.30	0.21	1.5	0.09
2B.....	400 KCl	Corn	4.75	0.62	0.14	4.5	0.18
2C.....	4000 $CaCO_3$	Corn	5.95	0.44	0.23	1.8	0.35
3B.....	400 KCl	Corn	8.00	0.65	0.10	6.2	0.40
3C.....	4000 $CaCO_3$	Corn	6.80	0.58	0.20	2.7	0.27
4B.....	400 KCl	Corn	6.28	0.77	0.10	7.6	0.15
4C.....	4000 $CaCO_3$	Corn	6.25	0.60	0.24	2.3	0.20
1B.....	400 KCl	Wheat	5.80	0.78	0.17	4.4	0.01
1C.....	4000 $CaCO_3$	Wheat	2.70	0.49	0.28	1.8	0.73
2B.....	400 KCl	Wheat	2.30	0.77	0.18	4.2	0.42
2C.....	4000 $CaCO_3$	Wheat	3.81	0.57	0.41	1.2	0.76
3B.....	400 KCl	Wheat	4.32	0.61	0.19	3.1	0.59
3C.....	4000 $CaCO_3$	Wheat	2.66	0.21	0.42	0.5	0.82
4B.....	400 KCl	Wheat	3.82	0.70	0.10	7.0	0.47
4C.....	4000 $CaCO_3$	Wheat	4.47	0.31	0.99	1.3	0.71
1B.....	400 KC.	Oats	4.87	1.24	0.22	5.8	0.02
1C.....	4000 $CaCO_3$	Oats	2.76	0.99	0.25	4.0	0.80
2B.....	400 KCl	Oats	2.10	0.97	0.09	10.0	0.06
2C.....	4000 $CaCO_3$	Oats	3.70	0.49	0.20	2.5	0.87
3B.....	400 KCl	Oats	3.12	0.64	0.20	3.2	0.20
3C.....	4000 $CaCO_3$	Oats	2.50	0.32	0.40	0.9	0.56
4B.....	400 KCl	Oats	3.70	0.78	0.14	5.3	0.49
4C.....	4000 $CaCO_3$	Oats	3.24	0.65	0.19	3.6	0.36

tionable than the original acidity. When quantities of potassium held by colloids are small, heavy liming would be necessary to liberate sufficient potash to be of use to plants. Potassium chloride also has been known to increase the alkalinity of soils, especially those

containing lime, as shown by MORSE (**16**). Analyses given in this report show the variability of potassium in plant tissues and its tendency to depress calcium content. Responses such as these in colloidal soils may account for many apparently contradictory results of numerous investigators on the effect of lime in liberating potassium. The desirable concentration of colloids varies with the chemical content of the soil and the crop to be raised. These conditions in turn should indicate the fertilizer practices to be employed. We need more information on the reasons for the great variability in concentration of elements in soils and tissues, and the rôle of various elements in metabolism in order to determine the kind and quantity of fertilizers to be applied to the soil.

Conclusions derived from chemical examination of tissues without consideration of soil factors are no more reliable than those derived only from soil analyses, and it seems imperative to have thorough knowledge of both soils and crops before conclusions may be made with any degree of reliability. The difference in behavior of clover and cereals on the same soils similarly treated indicates the necessity for knowing fertilizer needs of various crops. It seems safe to assume that these demands vary widely with type of crop and soil. Lysimeter experiments involving study of soil and plants in order to follow changes in them subsequent to use of fertilizers certainly point the way. Not until all factors are known is it judicious to try to select any one of them as an index to others, as it is possible that no factor or nutrient ratio is at all times and under all circumstances predominantly important.

Summary

1. Crops on acid muck soils chemically deficient in lime or potash may be injured by these elements in fertilizers. Clover is frequently injured by potassium.

2. Potassium increased stem erectness.

3. Use of calcium carbonate as fertilizer depressed the potassium content and the K/Ca ratio in crops grown on acid mucks.

4. High yields of clover showed a low K/Ca ratio in tissues. Crop yield of cereals was not dependent on the value of the K/Ca ratio.

5. Injuries following lime and potash applications to the soil are marked internally by depression of organic nitrogen and carbohydrate content.

6. Antagonism of ions between lime and potash was not observed, that is, neither eliminated the injurious effects of the other.

7. High nitrate nitrogen is associated with high calcium content of tissues and low crop yield.

8. High crop yield is associated with high organic nitrogen and high total carbohydrate content.

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SALT REQUIREMENTS OF WHEAT AT DIFFERENT GROWTH PHASES

W. F. GERICKE

(WITH TEN FIGURES)

Whether or not the salt elements needed for normal growth of vegetation must be present in the culture media of plants for all phases of their development, obviously is of great import in any study that pertains to the relation of the growth of the plant to the composition of the culture media. That the rates of absorption of material by plants change with their progressive development has been shown by numerous experiments. Thus it was found that absorption of inorganic elements by cereals is much greater during the early periods of their growth, when vigorous leaf production prevails, than when the heads form, or even for much earlier growth phases. These circumstances suggest that the composition of the culture media may be markedly altered during progressive growth of plants, without detriment to their ultimate development. To what extent this alteration in the composition of a complete nutrient solution could be extended to comprise a medium devoid of some of the essential elements, obviously would have singular importance in any study of the salt requirement and fertilizer needs of a plant. It occurred to the writer that experiments could easily be conducted that would throw light on this important matter. Plants could be started in complete nutrient solutions, and allowed to grow for a certain time. After having attained certain stages of development, they could be transferred to nutrient solutions devoid of one of each of the elements found in complete nutrient solutions, and there allowed to complete their growth. Likewise, plants could be started in partially complete nutrient solutions, allowed to grow for certain lengths of time, and then could be transferred into the complete nutrient solutions. From such experimentation, cultures would be obtained that were exposed to nutrient media in which one or more of each of the essential elements were absent for different lengths of time and for different stages of development of the plant.

FIG. 1.—Cultures nine weeks old, reading from left to right (in sets of three): set 1, complete, except potassium; set 2, plants grown first four weeks in medium of set 1, and then transferred to complete (set 4); set 3, plants grown first six weeks in complete nutrient solution (set 4), and then transferred to complete growth in solution of set 1; set 4, complete nutrient solution.

FIG. 2.—Cultures twelve weeks old, reading from left to right (in sets of two): set 1, complete except potassium; set 2, plants grown first four weeks in medium of set 1, and then transferred to complete (set 4); set 3, plants grown first six weeks in complete nutrient solution (set 4), and then transferred to complete growth in solution of set 1; set 4, complete nutrient solution.

FIG. 3.—Cultures twelve weeks old, reading from left to right (in sets of two): set 1, complete, except calcium; set 2, plants grown first four weeks in set 1, and then transferred to complete (set 4); set 3, plants grown first eight weeks in complete, and then transferred to medium of set 1 (note abnormality of heads), no grain produced; set 4, complete nutrient solution.

This paper contains some of the results obtained from such investigations.[1] Owing to the large number of chemical analyses yet to be made, which are necessary to give full interpretation to the results obtained, this paper will be confined to a presentation of photographs and some data as to weights of plants, to indicate the effects of the treatments on growth.

Briefly, the physiological part of the experiments was as follows: A large number of two-quart Mason jars were filled with culture solutions prepared from the following salts:

(1) Complete nutrient solutions: KH_2PO_4, $Ca(NO_3)_2$, $MgSO_4$.
(2) Nutrient solutions minus potassium: $Ca(NO_3)_2$, $MgHPO_4$, $MgSO_4$.
(3) Nutrient solutions minus calcium: KH_2PO_4, KNO_3, $MgSO_4$.
(4) Nutrient solutions minus iron: KH_2PO_4, $Ca(No_3)_2$, $MgSO_4$.
(5) Nutrient solutions minus magnesium: KH_2PO_4, $Ca(NO_3)_2$, $CaSO_4$.
(6) Nutrient solutions minus phosphorus: KNO_3, $Ca(NO_3)_2$, and $MgSO_4$.
(7) Nutrient solutions minus nitrogen: KH_2PO_4, $CaSO_4$, $MgSO_4$.
(8) Nutrient solutions minus sulphur: KH_2PO_4, $Ca(NO_3)_2$, $MgHPO_4$.

All nutrient solutions were composed of equal partial molecular concentrations of the salts indicated, and were of osmotic value equal approximately to one atmosphere pressure. The H-ion concentration of these different nutrient solutions varied between P_H 5.7 and 6.7. Wherever adjustments had to be made, salts were used that did not introduce any ions other than those indicated in each of the respective combinations named.

The containers were set with wheat seedlings 4–6 cm. high, and each culture contained five plants. At regular intervals, or when needed, distilled water was added to the cultures to make good the losses that had occurred through transpiration. Likewise iron in small quotas (applications of 0.5 cc. of 0.01 mol. $FeSO_4$) was added at sufficiently frequent intervals to maintain a proper supply of this material to all cultures except those where the plan called for its exclusion.

At different intervals, beginning with four weeks after the seedlings were set, cultures grown in the complete nutrient solutions were

[1] Two papers have appeared: The beneficial effect to wheat growth due to depletion of available phosphorus in the culture media (Science **60**:297–298. 1924), and The beneficial effect to plant growth of the temporary depletion of some of the essential elements in the soil (Science **59**:321–324. 1924).

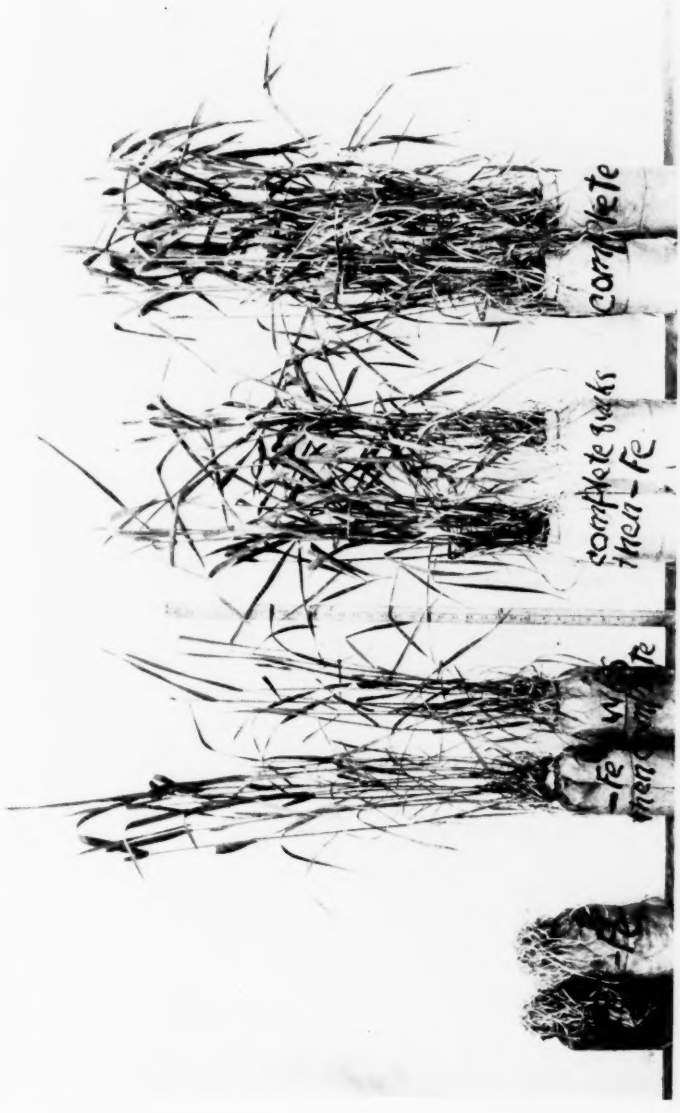

FIG. 4.—Cultures twelve weeks old, reading from left to right (in sets of two): set 1, complete, except iron; set 2, plants grown first four weeks in set 1, and then transferred to complete (set 4); set 3, plants grown first eight weeks in complete, and then transferred to medium of set 1; set 4, complete nutrient solution.

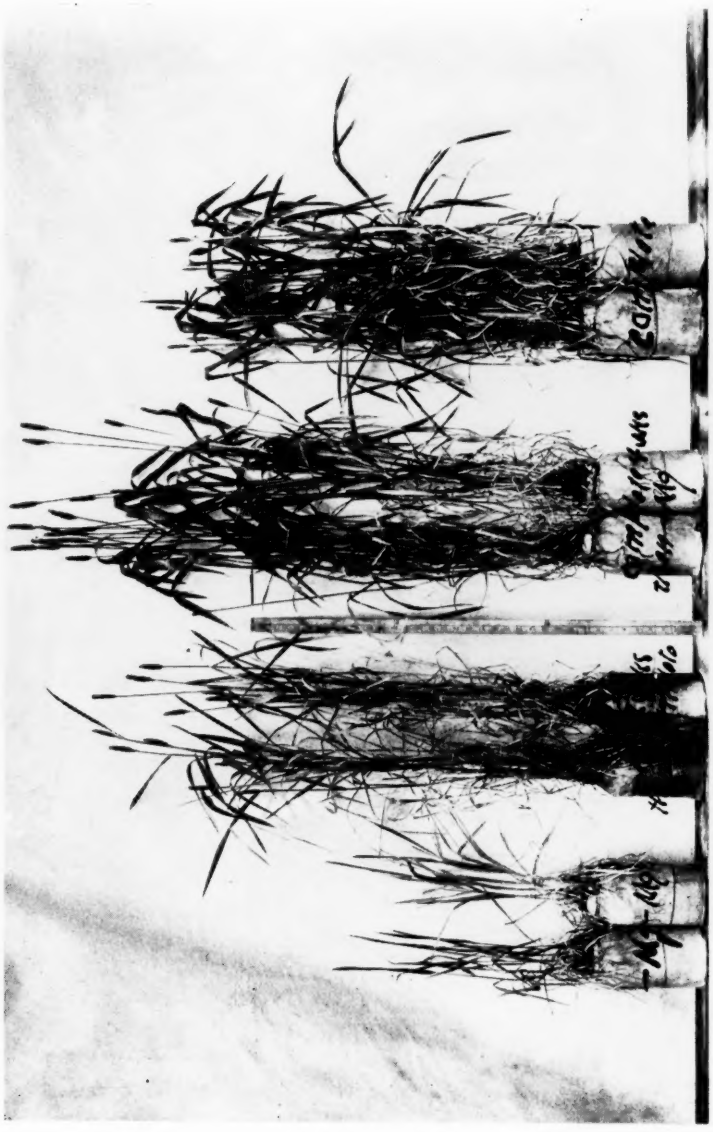

FIG. 5.—Cultures twelve weeks old, reading from left to right (in sets of two): set 1, complete, except magnesium; set 2, plants grown first four weeks in set 1, and then transferred to complete (set 4); set 3, plants grown first four weeks in complete, and then transferred to set 1; set 4, complete nutrient solution.

and then transferred to complete (set 4); set 3, plants grown first four weeks in complete, and then transferred to set 1; set 4, complete nutrient solution.

FIG. 6.—Cultures nine weeks old, reading from left to right (in sets of three): set 1, complete, except phosphorus; set 2, plants grown first four weeks in medium of set 1, and then transferred to complete (set 4); set 3, plants grown first four weeks in complete, and then transferred to medium of set 1; set 4, complete nutrient solution.

transferred to the partially complete solutions, and those of the latter to the former. Thus plants grown one month in complete nutrient solutions were placed in culture media in which one of the following elements was absent: K, Ca, Fe, Mg, P, N, and S, and allowed to complete their growth. Likewise, cultures deprived of one of each of these elements for the various fractions of their first growth period, were transferred to media containing the lacking element, and then allowed to complete their growth cycle. In addition to these treatments, two sets of cultures grown in complete nutrient solutions were treated as follows: one was transferred three times into new complete nutrient solutions, and the other was continued in the solution unchanged, in order to have data for comparison of the effect of frequently renewed culture media, that is, media relatively little unchanged by plants, with that changed by plants, because it was not renewed.

The investigation was carried out in the greenhouse. Tests were made of the solutions at intervals to ascertain the reaction of the media, as well as the approximate supply of all elements, in order to preclude any deficiency of elements contrary to the plan as stated. It was found that, in addition to iron, which was rapidly depleted, nitrogen would have been depleted in about 8–10 weeks' growth in the cultures grown in complete nutrient solution unchanged. Consequently, addition of nitrate was made to such cultures before the original supply was exhausted. Because of the very small amount of growth made by the cultures started in the partially complete nutrient solutions, except those devoid of sulphur and magnesium, which made considerable growth (but much less than that of the completes), it is obvious that by the transfer of the cultures from the completes to the partially complete culture media, practically a new supply of material was made available. Hence, with the exception of the cultures started in media devoid of sulphur and magnesium, no additions of nitrate were required to any transferred culture.

The plants were harvested when mature, and the weight of straw, grain, and roots determined. The results are given in table I.

The following conclusions are drawn from the data:

(1) After plants were exposed the first four weeks to complete nutrient solution, and had attained approximately one-seventh of

TABLE I

DRY WEIGHT OF WHEAT GROWN FIRST IN COMPLETE NUTRIENT SOLUTION, THEN TRANSFERRED TO NUTRIENT SOLUTIONS CONTAINING ALL ELEMENTS EXCEPT ONE AS INDICATED (VALUES AVERAGE OF 5 CULTURES, 25 PLANTS PER TREATMENT)

ELEMENT ELIMINATED FOR EACH SERIES	STRAW (GM.)	GRAIN (GM.)	ROOTS (GM.)	TOTAL (GM.)
	Set I: grown 4 weeks in complete nutrient solution before being transferred; approximate dry weight when transferred 4.6 gm.			
K	23.9	8.4	1.3	33.6
Ca	14.8	1.6	1.3	17.7
Fe	7.9	.....	1.1	9.0
Mg	32.0	8.0	3.2	43.2
PO_4	35.4	14.0	1.8	51.2
N	17.9	3.1	1.6	22.6
SO_4	27.4	10.0	2.3	39.7
	Set II: grown 6 weeks in complete nutrient solution before being transferred; approximate dry weight when transferred 5.7 gm.			
K	31.2	9.5	1.2	41.9
Ca	22.1	.....	1.3	23.4
Fe	11.5	.....	1.4	12.9
Mg	29.5	8.5	3.1	41.1
PO_4	30.7	9.8	1.2	41.7
N	18.6	4.2	1.3	24.1
SO_4	31.1	9.1	1.6	41.8
	Set III: grown 8 weeks in complete nutrient solution before being transferred; approximate dry weight when transferred 8.1 gm.			
K	26.3	8.8	1.3	36.4
Ca	20.0	.....	2.1	22.1
Fe	18.9	1.3	1.6	21.8
Mg	32.1	9.5	2.8	44.4
PO_4	29.3	10.1	1.4	40.7
N	19.5	3.8	2.4	25.7
SO_4	26.2	8.3	1.8	36.3
	Set IV: grown 10 weeks in complete nutrient solution before being transferred; approximate dry weight when transferred 9.5 gm.			
K	24.3	6.2	1.4	31.9
Ca	18.1	4.5	1.5	24.1
Fe	25.6	2.6	1.9	30.1
Mg	30.0	5.0	2.4	37.4
PO_4	24.6	5.6	1.2	31.4
N	19.3	4.1	2.1	25.5
SO_4	27.1	6.4	1.5	35.0
	Control: average of 10 cultures grown to maturity in complete nutrient solution thrice renewed			
	24.4	5.5	2.1	32.0
	Control: average of 10 cultures grown to maturity in complete nutrient solution, not renewed except by addition of 10 cc. of mol. sol. $Ca(NO_3)_2$ per culture when plants were about 8 weeks old			
	27.9	9.4	1.7	39.0

FIG. 7.—Cultures twelve weeks old, reading from left to right (in sets of two): set 1 complete, except phosphorus; set 2, plants grown first four weeks in medium of set 1, and then transferred to complete (set 4); set 3, plants grown first four weeks in complete, and then transferred to medium of set 1; set 4, complete nutrient solution.

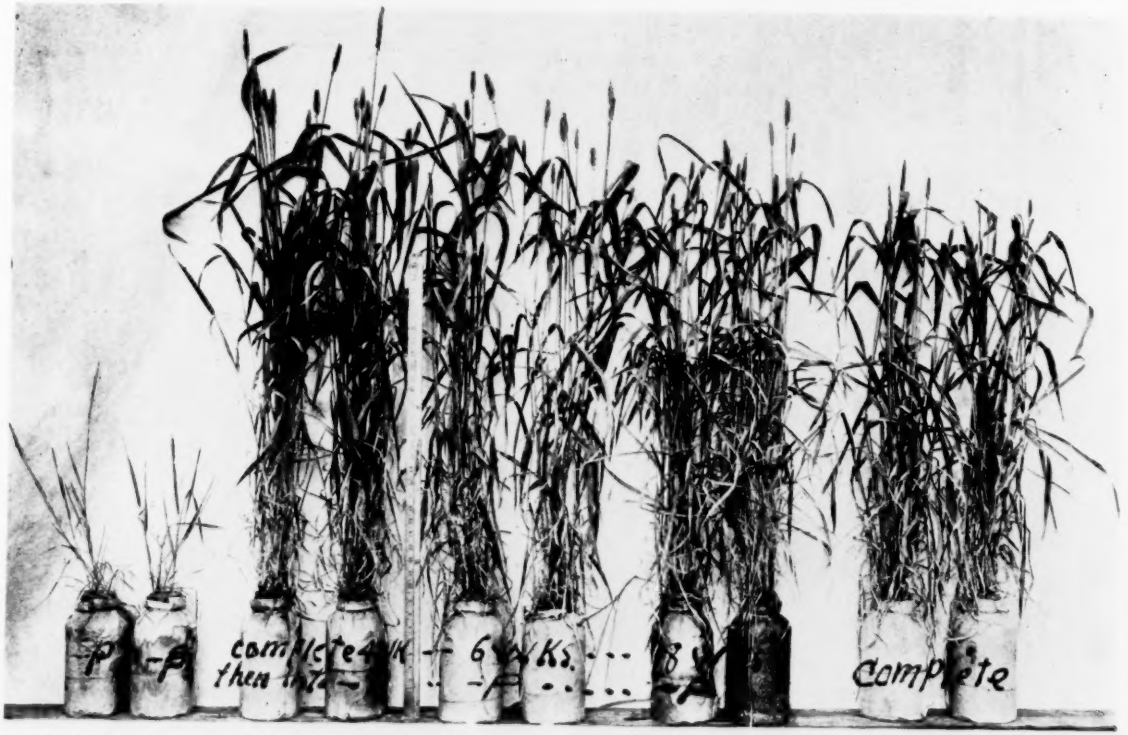

FIG. 8.—Cultures twelve weeks old, reading from left to right (in sets of two): set 1, complete, except phosphorus; set 2, plants grown first four weeks in complete, and then transferred to medium of set 1; set 3, plants grown first six weeks in complete, and then transferred to medium of set 1; set 4, plants grown eight weeks in complete, and then transferred to medium of set 1; set 5, complete nutrient solution.

the development (expressed in terms of dry weight) obtainable in such media, and were then transferred to media devoid of magnesium, phosphorus, or sulphur, they produced markedly more grain and straw than did the plants that grew to maturity in complete nutrient solution which was thrice renewed.

(2) Cultures grown six weeks in complete nutrient solution, and having attained approximately one-fifth of the dry weight of produce obtainable from such media, upon transfer to nutrient solutions devoid of potassium, markedly outgrew the cultures kept in complete nutrient solutions which were occasionally renewed. The removal of cultures grown four weeks in complete nutrient solution to a potassium-free medium resulted in dry matter production equal to that obtained from cultures grown in complete nutrient solution which was thrice renewed.

(3) The elements required longest in available form in the growth media for normal development of wheat are calcium and iron. Premature death occurred to the cultures deprived of iron after four to six weeks' growth in complete nutrient solution. Deprivation of iron in cultures grown eight or ten weeks in complete nutrient solution markedly inhibited grain production, the effect being more pronounced in the eight week case than in the ten week case. The removal of cultures (grown four, six, or eight weeks in complete nutrient solution) to media devoid of calcium markedly decreased total dry weight, and practically precluded grain production. The heads produced by the plants deprived of calcium, grown eight weeks in complete nutrient solutions, showed marked abnormalities. Cultures deprived of calcium, grown ten weeks in complete nutrient solution, produced nearly a normal amount of grain, but from its appearance it was judged to be very low in protein.

(4) The removal of cultures grown four, six, eight, or ten weeks in complete nutrient solutions to media devoid of nitrogen curtailed dry matter production, both of grain and straw, but otherwise the plants appeared normal. Good grain, although low in protein, judging from its appearance, was obtained from the cultures which were four weeks old when deprived of nitrogen.

(5) The maximum development among all cultures was obtained from the plants grown four weeks in complete nutrient solution and

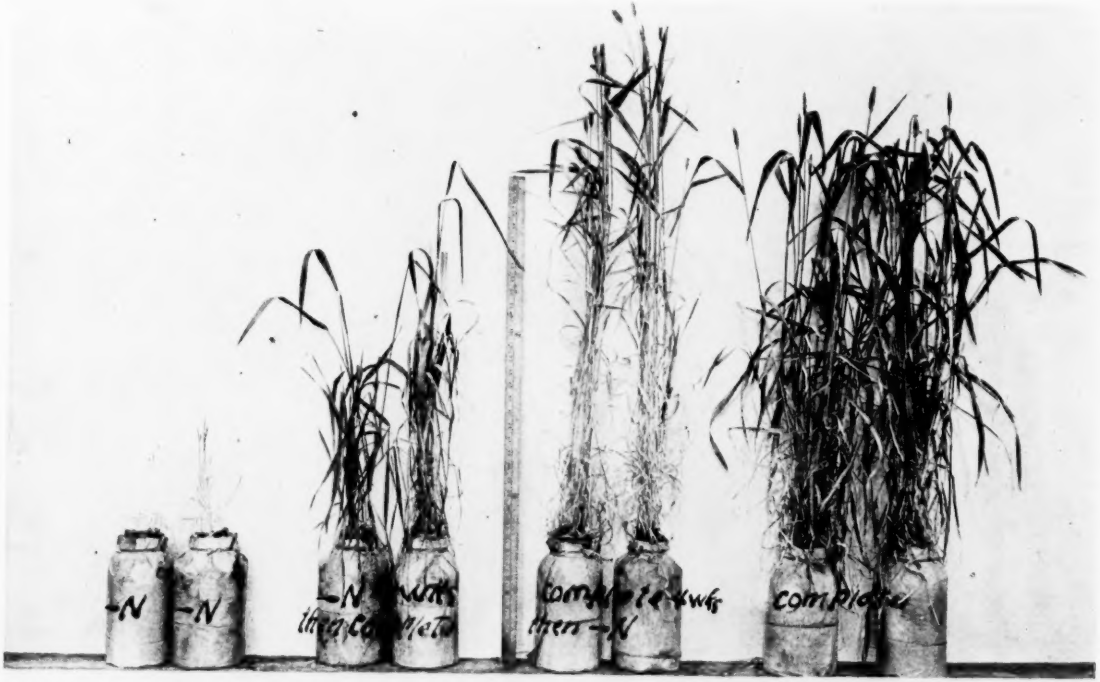

FIG. 9.—Cultures twelve weeks old, reading from left to right (in sets of two): set 1, complete, except nitrogen; set 2, plants grown first four weeks in medium of set 1, and then transferred to complete (set 4); set 3, plants grown first four weeks in complete, and then transferred to medium of set 1; set 4, complete nutrient solution.

FIG. 10.—Cultures twelve weeks old, reading from left to right (in sets of two): set 1, complete, except sulphur; set 2, plants grown first four weeks in medium of set 1, and then transferred to complete (set 4); set 3, plants grown four weeks in complete (set 4), and then transferred to medium of set 1; set 4, complete nutrient solution.

then transferred into media devoid of phosphorus, in which they grew 104 days.

(6) Better growth was obtained from the cultures grown to maturity in complete nutrient solution which was not renewed, than was obtained from cultures grown in complete nutrient solution which was thrice renewed.

(7) Supraoptimal exposure of cultures to complete nutrient solution of plants transferred to media devoid of K, Mg, P, or S, was inhibitory to maximum development of the plants. The effect of the excess was most noticeable with phosphorus and least with sulphur.

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set 1, and then transferred to complete (set 4); set 3, plants grown four weeks in complete (set 4), and then transferred to medium of set 1; set 4, complete nutrient solution.

DEVELOPMENT OF THE SEED OF ASPARAGUS OFFICINALIS[1]

W. W. Robbins and H. A. Borthwick

(WITH FORTY-THREE FIGURES)

In a study[2] having to do with methods of hastening the germination of common asparagus seeds, it became necessary to determine the stages in the development of certain seed structures. This investigation was later extended, and the results are here presented.

The seed of common asparagus arises from an anatropous ovule, two ovules normally being borne in each of the three locules of the ovary. The seed coat is black, finely rugose, and somewhat brittle. The embryo is a slender, threadlike structure completely imbedded in the hard, horny endosperm, the walls of which are hemicellulose. The structure of the mature seed of asparagus is briefly described and figured by Harz.[3] His descriptions and figures, however, show certain errors, which undoubtedly were due to his failure to follow through the changes which the seed structures undergo in their development. For example, he regards the structureless membrane just beneath the seed coat as the "epidermis of nucellus," whereas developmental studies show this to be of integumentary origin.

Both paraffin sections and sections of fresh seeds were employed. The latter were found to be particularly helpful. All drawings were made with a camera lucida.

Integument

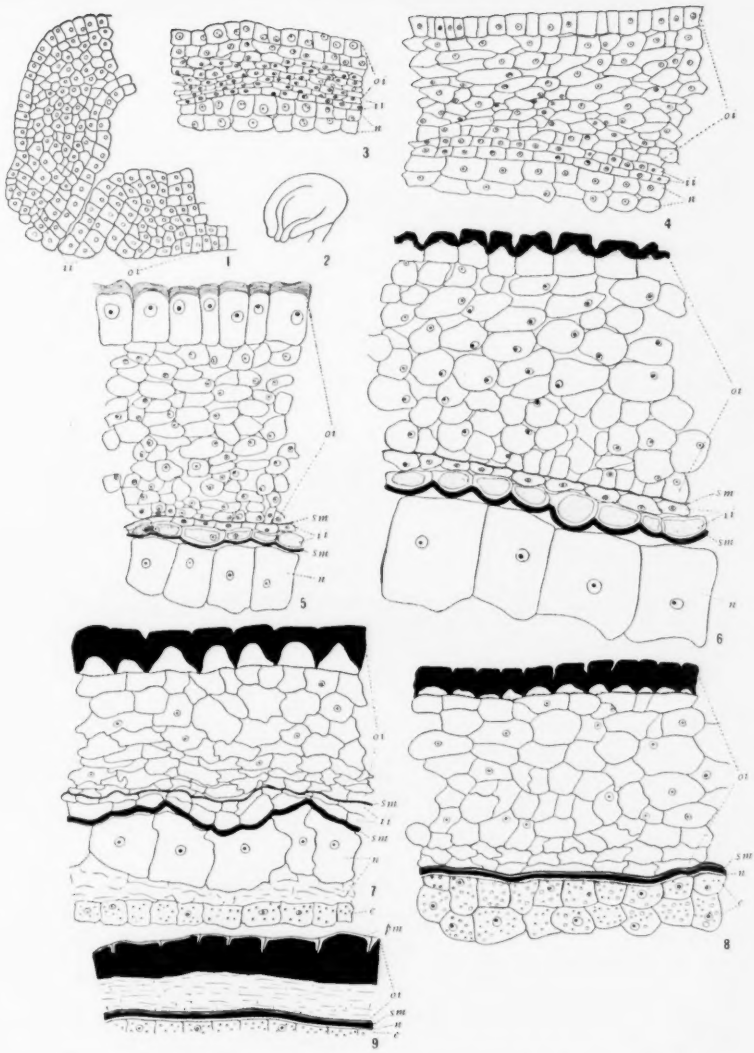
At the time of pollination, the inner integument of the ovule consists of two cell layers, and the outer integument of from five to ten layers (figs. 1–3).[4] The line of demarcation between the integuments

[1] Contribution from the Division of Botany, College of Agriculture, University of California.

[2] Borthwick, H. A., Factors influencing the rate of germination of the seed of *Asparagus officinalis*. Calif. Agric. Exp. Sta., Tech. Paper 18. 1925.

[3] Harz, C. D., Landwirtschaftliche Samenkunde. 1885.

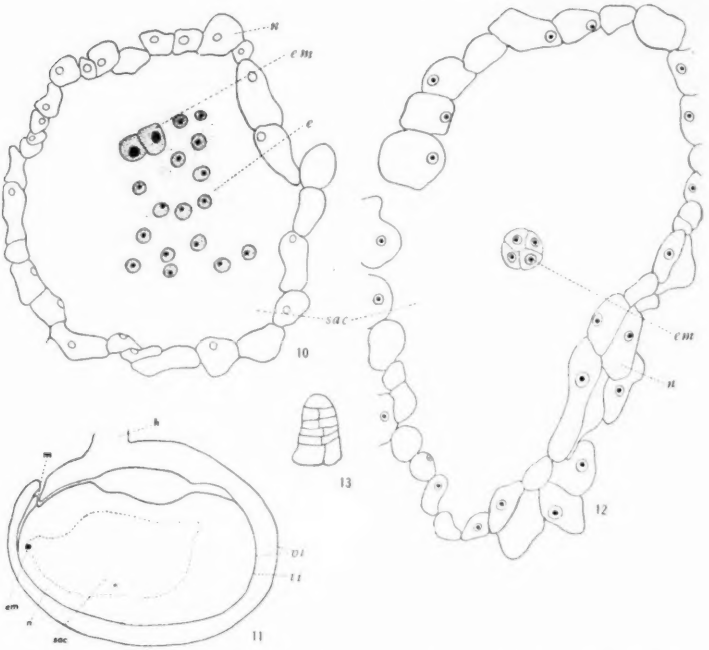
[4] In all the figures of this paper the following indicators are used: *de*, disintegrating endosperm cells; *e*, endosperm; *em*, embryo; *gr*, stem growing point; *h*, hilum; *ii*, inner integument; *m*, micropyle; *n*, nucellus; *oi*, outer integument; *pc*, pitted, thick walled endosperm; *pm*, pectic membrane; *r*, root tip; *rc*, root cap; *s*, seed coat; *sac*, embryo sac; *sm*, suberized membrane; *su*, suspensor; *tc*, thin walled endosperm cells.



FIGS. 1–9.—Sections showing stages in development of seed coat: fig. 1, integuments of ovule at time of pollination; fig. 2, diagram of anatropous ovule; fig. 3, 6 days after pollination; fig. 4, 8 days after pollination; fig. 5, 10 days after pollination; fig. 6, 16 days after pollination; fig. 7, 20 days after pollination; fig. 8, 29 days after pollination; fig. 9, mature seed; thickness of epidermis varies from one part of seed to another; it was not possible in every instance to secure comparable sections from seeds of different ages, a fact which explains in part the discrepancy in size of epidermal cells from seeds of approximately same age; all figs. except no. 2, ×168.

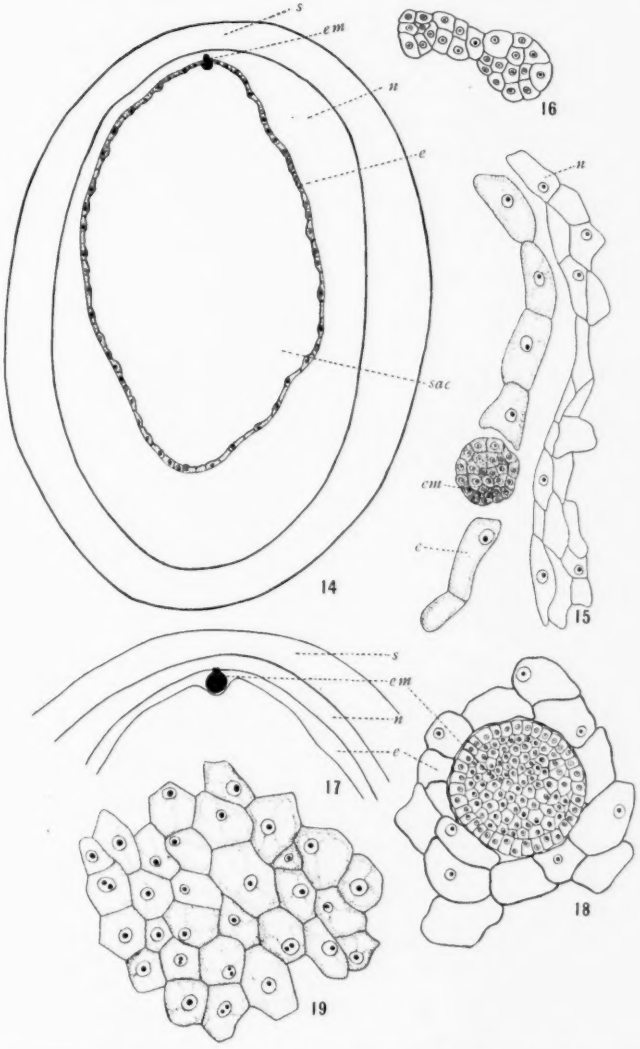
is sharpest near the micropyle. Here inner integument cells are much larger than they are posteriorly.

Within about sixteen days after pollination, the seed coat has reached its maximum thickness. The changes during this interval



FIGS. 10–13.—Fig. 10, section through micropylar end of embryo sac, 5 days after pollination; fig. 11, section of fresh seed taken 8 days after pollination; fig. 12, section through micropylar end of embryo sac 8 days after pollination; fig. 13, embryo dissected from fresh seed; figs. 10, 12, and 13, ×200; fig. 11, ×18.

are shown in figs. 1–6. There is a marked increase in the size of all cells of both integuments; the outer wall of the epidermal cells shows pronounced thickening; the two cell layers of the inner integument become easily discernible from the outer integument; the innermost cell layer of the inner integument becomes conspicuous because of the yellowish granular character of its cell contents, and because of the development of a membrane on its inner wall, adjacent to the



FIGS. 14–19.—Fig. 14, section of seed 13 days after pollination; fig. 15, section through embryo 13 days after pollination; fig. 16, embryo 13 days after pollination; fig. 17, section of seed 15 days after pollination; fig. 18, section of embryo 15 days after pollination; fig. 19, endosperm cells 15 days after pollination; figs. 14 and 17, ×20; all others, ×200.

nucellus; the inner boundary of the outer integument also becomes marked by a thin membrane. These two membranes give a pronounced fat reaction. VAN WISSELINGH[5] has found in the seeds of plants of many families that the two integuments and the innermost integument and nucellus are separated by "cuticles."

In subsequent developmental stages (figs. 7–9) it will be observed that there is a progressive desiccation and shrinkage of the cells, accompanied by compression due to the enlarging endosperm, with a consequent decrease in the thickness of the seed coat. The outer wall of the epidermal cells becomes very thick, the lumina of these cells being almost completely filled with a dark brown substance. Covering the outer surface of the epidermal cells is a thin, transparent membrane (fig. 9), which stains red with ruthenium red and violet with methylene blue. These color reactions indicate a pectic substance. This hydrophilous membrane which covers the surface of the seed probably facilitates the absorption of water.

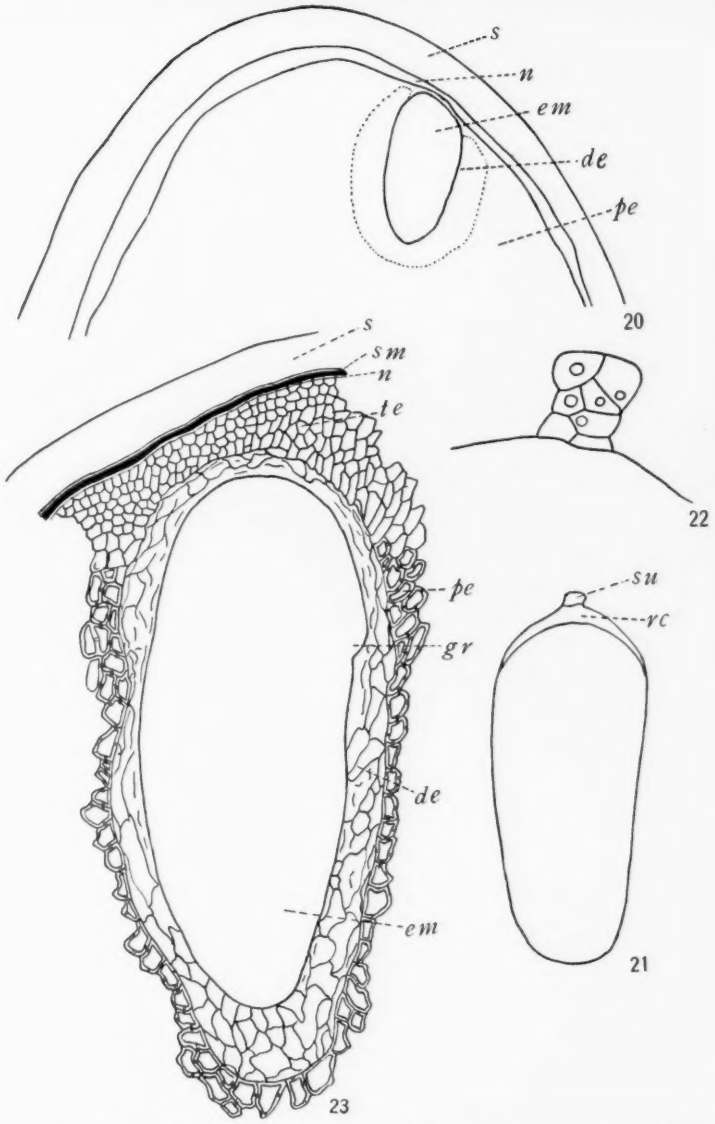
By about the thirtieth day following pollination the two fatty membranes are closely compressed (fig. 8). This condition has been brought about by the disintegration of the cells of the inner integument, accompanied by pressure on both sides. In the mature seed the membranes are usually indistinguishable, unless the tissues are treated with a solution of potassium or sodium hydroxide to bring about their swelling and separation.

This double membrane gives the following microchemical reactions: with Sudan III, a deep orange-red color; with methylene blue, a dark blue color; and with basic fuchsin, a red color, none of these colors fading in dilute acids or alcohol; ready dissolution when boiled in 2 per cent potassium hydroxide solution; and insolubility in 50 per cent chromic acid. That the membrane is of a fatty nature is well borne out by these tests. Studies, to be reported elsewhere, show that the semipermeability of the seed coat of asparagus is localized in this membrane.

Nucellus

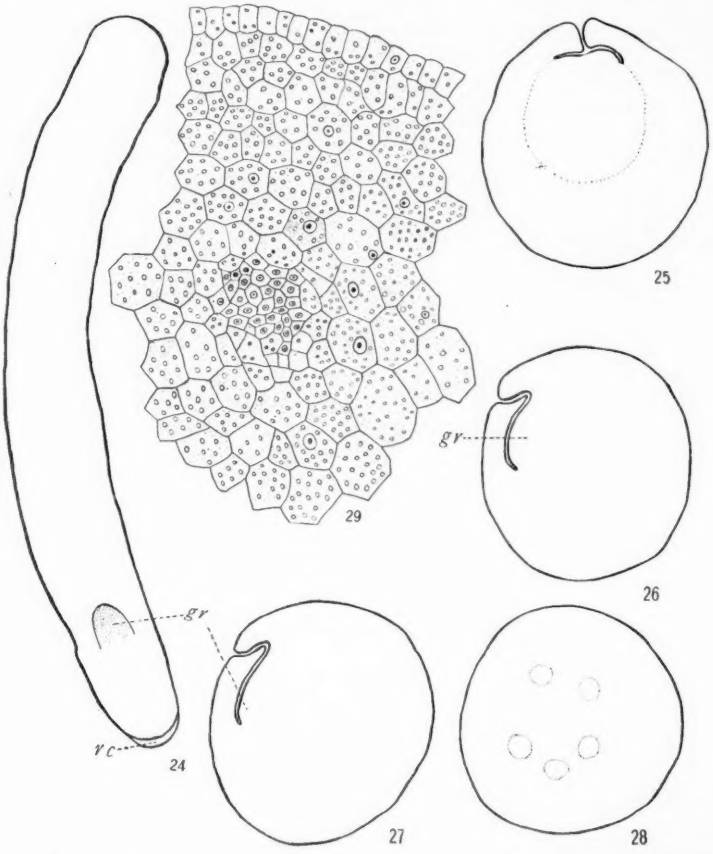
Contemporaneous with the enlargement of the seed coat, there is an increase in the size of nucellar cells. These attain their maxi-

[5] VAN WISSELINGH, C., Bijdragen tot de Kennis van de Zaadhind. Pharm. Weekblad **56**: 849–868; 1246–1271. 1919.



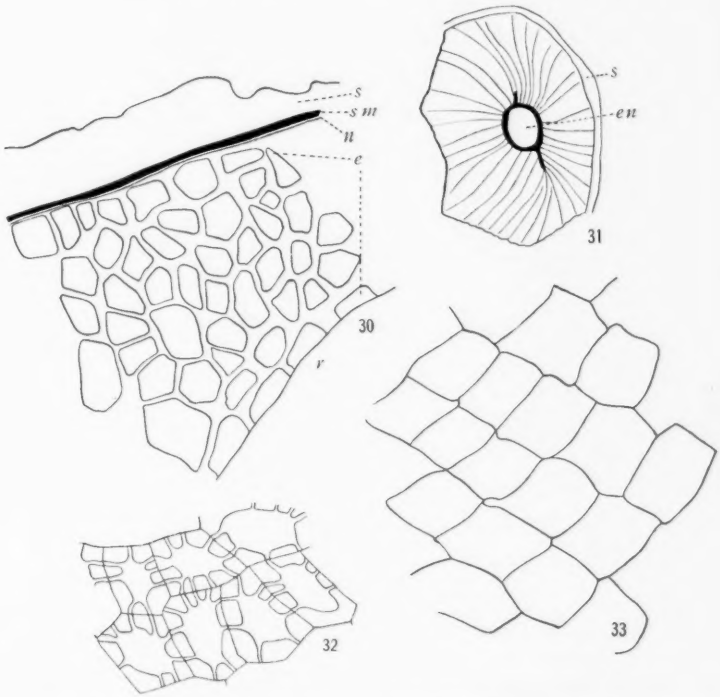
FIGS. 20–23.—Fig. 20, section of micropylar end 20 days after pollination; fig. 21, embryo 20 days after pollination; fig. 22, suspensor 20 days after pollination; fig. 23, section of seed 29 days after pollination, showing thin walled endosperm cells (*te*) in front of root tip, compressed and disintegrating endosperm cells (*de*) surrounding enlarged embryo, and pitted, thick walled endosperm cells (*pe*); fig. 20, ×31; figs. 21 and 23, ×62; fig. 22, ×330.

mum size about the sixteenth day after pollination. From this time the nucellar tissue becomes gradually disorganized and absorbed, its disappearance being initiated in the region bordering the endosperm (fig. 7). By the twentieth or twenty-first day, the encroaching endosperm has reduced the nucellus to a very narrow band of



FIGS. 24–29.—Fig. 24, external view of mature embryo; figs. 25–27, cross-sections through stem growing point; fig. 28, cross-section through cotyledon, showing 5 procambium strands; fig. 29, cross-section through portion of cotyledon, showing single procambium strand, and all cells filled with fat globules and protein granules; fig. 24, ×33; figs. 25–28, ×54; fig. 29, ×275.

compressed cells. Within about one month after pollination the nucellus is represented by a highly attenuated structureless layer, recognizable with difficulty unless properly stained (figs. 8, 23, 30).



FIGS. 30–33.—Fig. 30, section of mature seed, showing endosperm tissue just in front of root tip; fig. 31, diagram of section of mature seed, showing relation of embryo (*em*) to surrounding compressed and disorganized endosperm cells (solid black), radiating lines indicating radiating rows of endosperm cells; fig. 32, ordinary endosperm cells with thickened hemicellulose walls, middle lamella, and pits; fig. 33, endosperm cells after having been treated with 55 per cent sulphuric acid for 10 minutes; hemicellulose walls dissolved, leaving middle lamellae; ×260.

In the mature seed, the fragmentary remains of the nucellus show characteristic microchemical reactions. When a section of the seed is treated with 50 per cent H_2SO_4, the nucellus is the first to dissolve. With methylene blue, it gives a pronounced violet color,

and with ruthenium red a red color. These reactions indicate that the nucellus of the mature seed is pectic in nature.

Endosperm

The earliest stages in the development of the endosperm were not observed. On the fifth day following pollination, the endosperm was seen to be composed of a relatively small number of free nuclei, at the micropylar end of the seed (fig. 10). Rapid nuclear division ensues, and by the tenth day after pollination, endosperm nuclei are distributed quite uniformly throughout the peripheral region of the embryo sac (fig. 38), imbedded in a thin layer of cytoplasm. It is not until about the thirteenth or fourteenth day, however, that wall formation between endosperm nuclei begins (figs. 14, 15). Endosperm development now proceeds centripetally at a rapid rate, encroachment upon the embryo sac being approximately uniform from all sides. About three weeks after pollination, the endosperm tissue completely fills the embryo sac. At this time the embryo is relatively small (fig. 42). The storage of the endosperm with food reserves begins when the tissue is completely formed, and continues until the seed is ripe. The reserves are hemicellulose in the walls, and oil and protein in the lumina. Increase in the thickness of the walls of endosperm cells is first observed about the twenty-fifth day after pollination. Cell wall thickening takes place first in the innermost cells, and progresses centrifugally. As the walls thicken narrow canals are left at intervals, those of adjoining cells coinciding (fig. 32). Endosperm cells adjacent to the nucellus remain thin walled until the seed is almost mature.

Microchemical studies show that the middle lamellae of endosperm cells are of pectic substance, whereas the thickened walls are of hemicellulose. Forty-five per cent sulphuric acid dissolves the hemicellulose walls somewhat rapidly, 3 per cent sulphuric acid at room temperature slowly dissolves them, and 3 per cent sulphuric acid at boiling temperature dissolves the walls completely in from five to ten minutes. Chromic acid also causes slow dissolution. With methylene blue the thickened walls are stained a light blue, and stand out in marked contrast with the dark violet-blue of the middle lamellae. The middle lamella is stained red with ruthenium red, while the thickened portion of the wall is unstained.

The endosperm throughout is not homogeneous in its structure and chemical constitution. In sections cut parallel with the embryo, a fan-shaped group of endosperm cells spreads out from the root tip to the seed coat. These cells differ from the great mass of endosperm cells, and are characterized by their irregular cubical shape, the absence of pits, and the fact that the walls stain a very deep violet with methylene blue and pink with ruthenium red, indicating pectic material. The presence of this tissue, rich in pectic material, between the root tip and the seed coat, appears to be of advantage to the growing embryo at the time of germination. Such tissue not only absorbs water readily, but it is one through which the root tip can find comparatively easy penetration. In any section of the seed (taken about one month after pollination) which includes the embryo, the tissue immediately surrounding it is composed of endosperm cells in various stages of disorganization (fig. 23); it becomes structureless and apparently composed only of cellular membranes. There are also groups of cells radiating from the embryo (fig. 31) which are very thin walled, compressed, and partly disorganized. The walls of these cells, and also of the structureless tissue, give

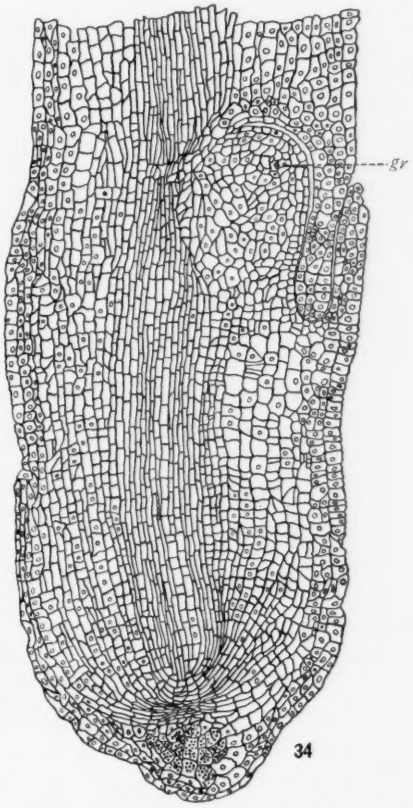


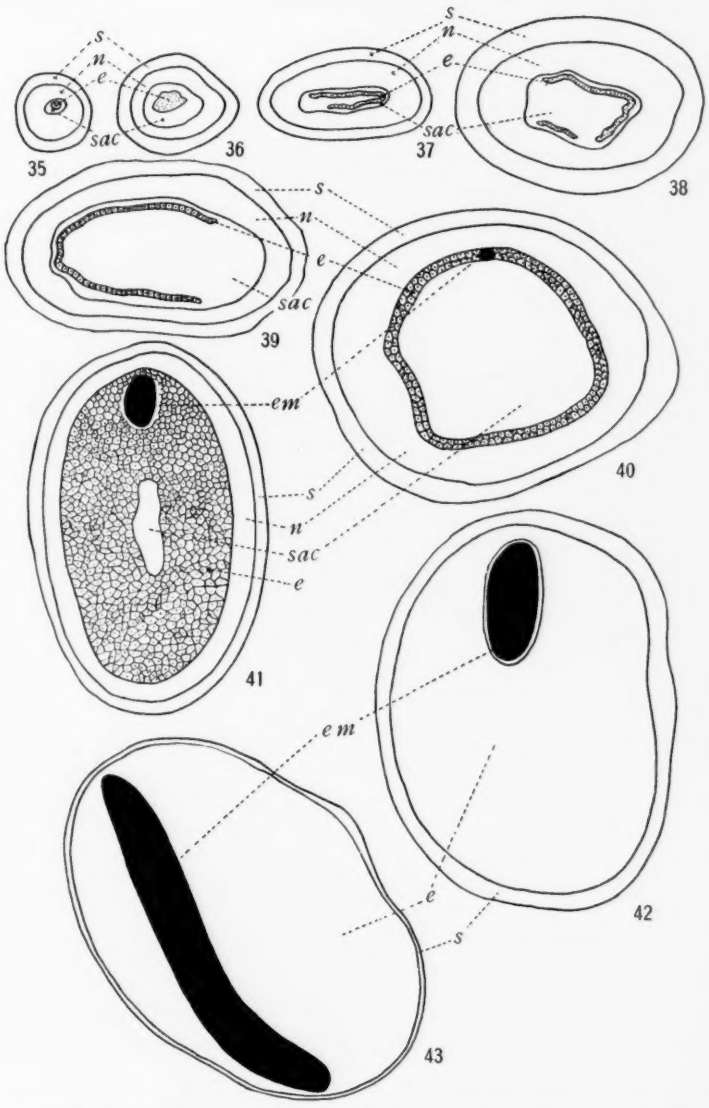
FIG. 34.—Longitudinal section of tip of embryo from mature seed; ×100.

color and solubility reactions which indicate that they are pectic substances.

Embryo

The earliest stage observed in the development of the embryo was as shown in fig. 10. About ten days after pollination, the proembryo could be observed in suitable sections of the fresh berry. Its position in the seed, and its size, relative to other seed structures, are seen in fig. 11. At this age the proembryo consists of an irregular shaped, rather massive suspensor of the *Lilium* type, and a few celled embryo. The suspensor is partly surrounded by nucellar tissue, and its attachment to the nucellus is firm enough to prevent the proembryo from being easily shaken loose in the ordinary handling of fresh sections on the microscope slide. Between the tenth and thirteenth day, the suspensor elongates somewhat, pushing the rapidly enlarging embryo into the cavity of the embryo sac (figs. 14, 17). By the second week the developing endosperm has completely surrounded the free end of the embryo (fig. 17). At no subsequent stage of its development does the embryo project freely into the cavity of the embryo sac. By the third week (figs. 20–23) the embryo has become an elongated, many celled structure. The root cap is visible, and a number of its cells possess starch grains. The suspensor is still attached to the embryo. As stated, immediately surrounding the enlarging embryo are rows of thin walled, compressed endosperm cells which by their appearance and behavior are different from the endosperm cells farther removed from the embryo. When fresh sections of the seed are first placed in water and examined, these cells are not noticeably different from other endosperm cells, but after standing in water for half an hour, there is a disorganization of the cells, the walls apparently dissolving, and all that remains are small aggregations of proteinaceous and fatty material.

During the fourth week there is a rapid increase in the size of the embryo. It becomes freed from the nucellus and completely invested by the endosperm. A lateral depression develops a short distance posterior to the root cap, within which the stem growing point is situated (fig. 23). The hypocotyl is short, and the cotyledon elongates so that the mature embryo is almost the full length of the seed. During germination the cotyledon remains in the seed in close



FIGS. 35–43.—Diagrams of 9 stages in development of seed: fig. 35, 5 days after pollination; fig. 36, 6 days after pollination; fig. 37, 8 days after pollination; fig. 38, 10 days after pollination; fig. 39, 13 days after pollination; fig. 40, 16 days after pollination; fig. 41, 20 days after pollination; fig. 42, 29 days after pollination; fig. 43, 44 days after pollination; ×15.

contact with the endosperm, acting as an absorbing and conducting organ.

It will be observed from an examination of figs. 23, 41, and 42 that the developing embryo is confronted with a thick walled endosperm tissue, through which it must make a path. It has already been pointed out that the endosperm cells immediately in front of the embryo appear to be in a state of disorganization; the walls of such cells give reactions indicating pectic substance. This situation continues throughout the growth of the embryo.

Mature seed

In the mature seed, the seed coat has a single, epidermal layer of cells, the outer wall of which is thick, the inner thin, and the lumina are almost completely filled with a dark brown material. A thin, transparent pectic membrane covers the outer surface of the epidermal cells. Beneath the epidermis are rows of highly compressed cells, the lumina of which appear as mere dark slits. Below these cells is a suberized membrane, separable into a thin and a thick membrane, closely compressed. These represent, respectively, the "cuticles" of the inner and outer integuments. Under the fatty double membrane is a narrow structureless zone, giving a pronounced pectic reaction, which represents the remnants of nucellar tissue. The bulk of the seed is composed of endosperm cells which have thick pitted walls of hemicellulose, and lumina well filled with protein granules and fat globules. The endosperm cells immediately surrounding the embryo, and also narrow strands of cells radiating from the embryo, are much compressed, and in various stages of disorganization. Endosperm cells between the root tip of the embryo and the nucellar zone are relatively thin walled and pitless, and the walls appear to be largely pectic in nature.

The mature embryo is a slender, threadlike structure completely imbedded in the endosperm. It is differentiated into root, with root cap, short hypocotyl, stem growing point, and elongated cotyledon.

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CONTINUITY OF PROTOPLASM IN ENDOSPERM CELLS OF DIOSPYROS[1]

EDUARDO QUISUMBING

(WITH PLATES XXIII, XXIV AND TWO FIGURES)

Introduction

This paper is an account of the results of a study of protoplasmic connections in the endosperm cells of *Diospyros discolor*, *D. ebenaster*, *D. Ahernii*, and *D. kaki*. The investigation was begun at the University of Chicago, and was completed in the Philippines.

Methods were developed for demonstrating protoplasmic connections in the endosperm cells of *D. discolor*, *D. Ahernii*, *D. ebenaster*, and *D. kaki*. Various attempts to perfect an indirect method for demonstrating continuity of protoplasm in vegetative and reproductive tissues have been only partially successful, as was found by GARDINER (3), TANGL (15), and many others, and also by the writer. While the present method proved to be satisfactory for the endosperm of *Phytelephas macrocarpa*, *D. discolor*, *D. Ahernii*, *D. ebenaster*, and *D. kaki*, it is unsuitable for the endosperm of some seeds, as, for example, *Cocos nucifera*. This difference in reaction is due to the chemical nature of the endosperm cells, and also to the thickness of the cell walls. The discovery of protoplasmic connections in the endosperm of all seeds would be important both for the physiologist and morphologist, as the results might throw some light on some of the complicated problems of the physiology of seeds.

Protoplasmic connections are known to occur in vegetative as well as in reproductive tissues, and have been observed in all the great divisions of plants, even in the lower Thallophytes. They have been described in the Cyanophyceae, fungi, and lichens. They have also been observed in *Volvox*, *Gonium*, *Spirogyra*, *Cladophora*, *Ulothrix*, *Mesocarpus*, and the Phaeophyceae. Continuity of protoplasm has been demonstrated in the Rhodophyceae, especially in the Florideae, in liverworts, in moss leaves, guard cells and stem, in Pterido-

[1] Read before the Los Baños Biological Club, October 28, 1924.

phytes, and in gymnosperms. In angiosperms the occurrence was proved by GARDINER (1–7), KUHLA (11), and many others. They occur in parenchyma cells of vegetative tissues, xylem and phloem, in nodes of grasses, and motile organs of the leaves, etc.

Although a voluminous literature exists on the continuity of protoplasm in vegetative tissues, there is very little on reproductive tissues, particularly the endosperm. TANGL (15) first demonstrated the existence of protoplasmic connections in ripe endosperm cells of *Strychnos nux-vomica*, *Areca oleracea*, and *Phoenix dactylifera*. He found that the cell walls in these species were perforated by fine protoplasmic threads. Six years later he (16) investigated the endosperm of grasses, and found that the aleurone and starch cells are in mutual connection by means of very fine protoplasmic threads passing through unpitted cell walls. MOORE (12) investigated the continuity of protoplasm through the cell walls of endosperm cells in several species of *Strychnos*, and of *Diospyros embryopteris* and *D. melanoxylon*. GARDINER'S (3) work on the protoplasmic connections in seeds appeared in 1883. He examined a number of monocotyls, especially palms, numbering fifty-three species, and dicotyls numbering twenty-nine species represented by eleven families. He pointed out also that the structure of the protoplasmic connections in various seeds presents every possible modification. He (5) studied the technique for demonstrating protoplasmic connections, and in 1897 published his results on *Tamus communis*, and also the interesting structure of the endosperm cells of *Lilium Martagon*. Others who have described protoplasmic connections in the endosperm are GARDINER and HILL (8, 9); STRASBURGER (14) who described and figured protoplasmic connections in the endosperm cells of *Phytelephas macrocarpa* and *Tamus communis;* KENITZ-GERLOFF (10); ZABRISKIE (19); STOPES and FUJII (13); and WULFF (17, 18). Besides these investigators, many have mentioned and figured protoplasmic connections of the endosperm in textbooks.

Development of technique

The history of the development of technique for demonstrating protoplasmic connections is so voluminous that only the principal methods can be mentioned.

TANGL (15), who first announced the existence of protoplasmic connections in Phanerogams in his work on the endosperm of *Strychnos nux-vomica*, *Areca oleracea*, and *Phoenix dactylifera*, treated his sections with iodine diluted with alcohol or with potassium iodide, and then mounted them in chloriodide of zinc. The connections stained dark brown and the cell walls yellow. He tried to use haematoxylin and carmine after fixing in iodine, but failed. He also treated his material with tincture of iodine. GARDINER (3) saw the threads clearly in the endosperm cells of *Bentinckia Conda-panna* by mounting sections in dilute glycerine. In the case of *Tamus communis*, he used osmic acid-uranium nitrate mixture (Kolossow's reagent) as a fixative, and preserved in thymol water for future use. Safranin alone or Hoffmann's blue was used for staining. Safranin may be followed by gentian violet or eosin. GARDINER also tried sections of endosperm, placed in water, treated with iodine, and mounted in chlorzinc iodide; washed in water stained with picric-Hoffmann's blue; mounted in glycerine or glycerine jelly. For *Strychnos* and *Tamus* he modified this method by placing sections in alcohol and treating with alcoholic iodine and mounting in glycerine. MOORE (12) reported seeing protoplasmic threads in the seeds of *Strychnos Ignatia* without fixing or staining, by simply placing sections of the hard dark endosperm in water. He succeeded in staining the threads better, however, by placing the sections in picric acid, washing, and then leaving them in Judson's Oxford blue for a few minutes, or washing in water or in strong or dilute glycerine. He showed threads in *Diospyros embryopteris* and *D. melanoxylon* by placing sections in chloriodide of zinc for twenty-four hours, and then washing, and staining them in picric blue. STOPES and FUJII detected "plasmodesma" in *Encephalartos Lehmanni*, *Zamia floridana*, and other material by using hand sections of alcoholic material, washing in water, treating for a short time with sulphuric acid, and then staining in aniline blue.

Procedure

Ripe seeds of *Diospyros kaki* were furnished through the courtesy of Dr. SHIGEO YAMANOUCHI of Tokyo Higher Normal School, Japan. These were preserved in ordinary formaldehyde, and were

washed in 50 per cent alcohol before cutting. The seeds of *D. discolor*, *D. kaki*, *D. Ahernii*, and *D. ebenaster* were cut fresh and also after preserving in formo-aceto-alcohol, or in 10 per cent formaldehyde.

The first difficulty encountered is the method of cutting, as all the seeds are more or less bone-hard. It was found also that the planes cut affected the ease of examining protoplasmic connections after mounting. The writer found exceptions in the case of *D. discolor* and *D. Ahernii*, where all planes showed perfectly clear protoplasmic connections. Of the four species of *Diospyros* so far studied, *D. discolor* and *D. Ahernii* were similar to *Strychnos Ignatia*. Protoplasmic connections may be seen in sections mounted in water under a high power dry objective.

Technique

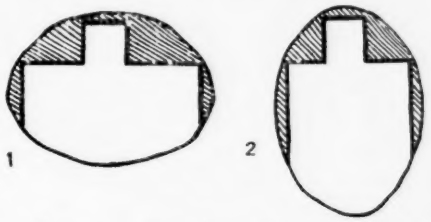
A Spencer sliding microtome or the rotary microtome was used for sectioning. Longitudinal radial sections of seeds (text fig. 1) show the best view for studying protoplasmic connections. In transverse sections (text fig. 2) the cells are elongated, except in *D. Ahernii*, in which the cells are isodiametric. *D. discolor* and *D. Ahernii* show the protoplasmic connections best, both in transverse and radial longitudinal sections.

Before the seeds are clamped on the microtome holder, they should be trimmed as illustrated in text figs. 1 and 2. The sections may be cut 5–15 μ, lifted with a camel's hair brush, and transferred into a dish containing the fixative. Fix in Bouin's fluid for forty-eight hours, and then wash in 50 per cent alcohol until the yellow color disappears from the liquid and the sections after washing. Two methods may be given for the next step.

1. From 50 per cent alcohol transfer the sections to alcoholic safranin and allow to stay for a day. Then wash sections in water to remove extra safranin, and stain further in aqueous gentian violet for four days; wash in water, pass through grades of alcohol (50, 95, and 100 per cent) at intervals of two minutes, then through clove oil and xylol, after which they may be mounted in Canada balsam. Safranin is prepared by dissolving 10 gm. of safranin crystals in 500 cc. of 95 per cent alcohol. The container is shaken and allowed

to stand over night. The next day the stain is transferred in a liter flask and filled up to the neck with distilled water, and then filtered. Gentian violet is prepared by dissolving 5 gm. of the crystals in 500 cc. distilled water. After shaking thoroughly, and allowing to stand for a day, it is filtered.

2. The best stain for demonstrating protoplasmic connections in the endosperm cells of *Diospyros* is the Haidenhain's iron-alum haematoxylin. After washing the sections in 50 per cent alcohol, they should be transferred to water, passing through 30 and 10 per cent alcohol with ten minutes in each grade. All trace of alcohol should be washed out before putting sections in iron-alum. The sections should be placed in 2 per cent iron-alum for two hours, washed thoroughly in water, and then placed in 0.5 per cent haematoxylin over night. Haematoxylin used should ripen six weeks from the date it is prepared; very old haematoxylin is unsatisfactory. Sections are washed thoroughly in water the next morning, transferred to iron-alum, and then washed thoroughly in water before dehydrating. After washing use different grades of alcohol (10, 30, 50, 80, 95, 100 per cent) at five to ten minute intervals. The sections are then placed in gold orange dissolved in clove oil for about five minutes, into clove oil, and then into xylol, from which they are mounted in Canada balsam. Sections of endosperm from young seeds collapsed and shriveled when placed in xylol, so they were mounted in glycerine jelly after staining.



FIGS. 1, 2.—Fig. 1, front view of seed, showing method of obtaining longitudinal radial sections; fig. 2, side view, showing method of obtaining transverse sections.

Seeds

Diospyros discolor is endemic to the Philippines. The fruit is edible, and is covered by densely pubescent purplish brown hairs. The seeds are ellipsoid, one side flat and the other convex, 3–3.2 cm.

long, 2–2.3 cm. wide, and 1.3–1.5 cm. thick. The seed coat is thickest at the micropylar end (0.5–0.75 mm.), light reddish brown externally, but differentiated internally into a dark brown layer. The endosperm is white and hard, resembling that of *Phytelephas macrocarpa*, although a little softer.

Diospyros ebenaster is an introduced species, coming from Mexico during the early colonial period. It is now being cultivated, and is noted for its large edible fruits, which are smooth and green when mature, but turn brown when ripe. The edible pulp is yellowish, but soon turns black when ripe. The seeds are oblong, compressed, one side keel-shaped and the other thickened and more or less rounded, 2.2–2.5 cm. long, 1.2–1.5 cm. wide, and 7–9 mm. thick. The seed coat is thin and reddish brown in color. The endosperm is cream white, and in all essentials like *D. discolor* in texture.

Diospyros Ahernii is an endemic species. The fruits are pubescent, coated with yellow hairs. The pulp is thick and fibrous, and not very palatable. The edible portion of the fruit is the sweet gelatinous mass which covers the seeds. The seeds are shaped like *D. discolor*, with one side flat and the other convex, 2.5–2.6 cm. long, 1.0–1.3 cm. wide, and 8–10 mm. thick, orange brown in color. The seed coat is thin like that of *D. ebenaster*. The endosperm is white and somewhat hard in texture.

Diospyros kaki is a Japanese species. A few plants of this species are being cultivated in the Philippines, in the mountain province, island of Luzon. The seeds are hemi-ellipsoid to ellipsoid, 1.8–2.5 cm. long, 0.9–1.2 cm. wide, and 4–6 mm. thick. The seed coat is little thicker than that of *D. ebenaster*, but the color and texture of the endosperm resemble that species.

Endosperm cells

The seed is invested by a coat of several layers of parenchymatous cells (fig. 1), forming a more or less spongy testa. Beneath this coat the outermost cells of the endosperm are smaller and thinner than the underlying ones. The nuclei persist in nearly all of the cells.

The form and size of the endosperm cells are different in different species, and in different parts of the same endosperm. As previously

indicated, the cells are almost isodiametric in radial longitudinal sections of the endosperm, and are elongated horizontally in transverse sections, except in *D. Ahernii*, where all cells are isodiametric.

The following description of the endosperm cells is for *D. discolor*. It holds true for the other species studied with little variation, except *D. Ahernii*. The cells in the other species vary in size and thickness of the walls. In transverse sections of the endosperm (fig. 1) the form and size of the cells vary as the axis of the seed is reached. The cells adjacent to the coat are smaller and somewhat isodiametric, although the epidermal cells are more or less squarish. Some, however, are slightly elongated horizontally, and the corners are rounded. The cell walls are thinnest near the coat (6–10 μ), and thicken gradually toward the underlying cells. Thin walled cells may be seen also in the middle. No striations of any kind are evident in the walls. The nucleus is present and persists in the cells, near the periphery, but seems to be disorganized in the cells within. A great number of tiny rounded granules are imbedded in the cytoplasm. In *D. ebenaster* the cell inclusions are these tiny granules, but in addition there are large rounded globules of oil. The middle lamella is very prominent in cells near the periphery, but is present in all the cells. It is perforated by the protoplasmic connections. Three or four layers away from the periphery in transverse sections the cells begin to elongate, and are at their best several layers within, some even attaining the length of 130 μ, with tapering ends. The walls are 8–14 μ thick. The cells near the axis of the seed are less elongated, more or less isodiametric, with sharp corners and thickened walls, sometimes attaining a diameter of 18 μ.

In radial longitudinal sections the endosperm cells are nearly always isodiametric, except in *D. Ahernii*, with more or less rounded lumen, with the exception of those cells near the periphery, which in form and size resemble those of the transverse sections. The diameter of the lumen varies even in the same species.

Protoplasmic connections

Protoplasmic connections in the endosperm cells of *Diospyros* species studied may be classified under two main categories, those which occur in great numbers and those which are scanty, isolated,

and restricted. Of the four species studied, protoplasmic connections may be observed in two species without the aid of any fixative or stains, by simply mounting the sections in water. They are extremely delicate in *D. kaki* and in *D. ebenaster*, but are quite pronounced and thickened in *D. Ahernii* and *D. discolor*. Protoplasmic connections at the ends of the groups are generally thicker than those in the middle, measuring 0.5–0.55 μ. Some connections in the middle are also thickened like those at the ends, and this is especially true in the three species except *D. discolor*, which sometimes shows such thickening also at the ends. The thickness of the connections is exaggerated in the photomicrographs (figs. 7–10). The doubling situation of connections appears single in the photomicrographs.

The number of protoplasmic connections traversing the whole thickness of the unpitted cell walls varies according to the species. They are very numerous in *D. discolor* (figs. 1–3, 7), and in *D. Ahernii* (figs. 4, 8). The arrangement of the protoplasmic connections is well demonstrated in the elongated cells of *D. discolor* (figs. 1, 2). In *D. ebenaster* (figs. 5, 9) the protoplasmic connections crossing the walls are not so numerous, the minimum number being six. *D. kaki* has the least number of the four species (figs. 6, 10), sometimes as low as four traversing the walls. In all cases the number and identity of the protoplasmic connections seem to disappear toward the periphery (fig. 1). Very few protoplasmic connections are present in walls of cells near the coat.

The length of protoplasmic connections seems to vary greatly, and this variation is due to the thickness of the walls to be traversed. Protoplasmic connections away from the periphery are usually longer than those found traversing the walls of cells near the periphery, or thin walls anywhere. The form of the protoplasmic connections varies also. Those at the ends of groups are generally rounded or acute. The ones at the center are usually straight, and in elongated cells they are sometimes oblique in position. Protoplasmic connections occur either singly or in groups. When single they are generally thicker than those in groups. Groups of two are very common, while three, four, five, or six are rare, especially the five and six. Sometimes the protoplasmic connections coalesce, and when this occurs the connections seem to be very much thickened. In *D. discolor* and

D. Ahernii protoplasmic connections occur over the whole area of the cell walls. In *D. ebenaster* and *D. kaki* they are restricted to the middle of the cell walls, and very seldom occur at the corners. In none of the cases have any nodal swellings of the protoplasmic connections been observed. The groupings of the protoplasmic connections in *D. kaki* and *D. ebenaster*, and sometimes in the two other species, result in a barrel-shaped form.

Summary

1. Protoplasmic connections in *D. discolor* and *D. Ahernii* may be observed without the aid of fixation and stain.

2. The use of Bouin's fluid for killing and fixing the endosperm of *Diospyros* seeds is very satisfactory.

3. Haidenhain's iron-alum haematoxylin, counter stained with gold orange dissolved in clove oil, proved to be the best combination of stains. The cell walls were colored orange and the protoplasmic connections dark bluish brown.

4. Safranin gentian violet stains also proved satisfactory. The cell walls were colored pinkish red, with the protoplasmic connections violet.

5. The nature of the protoplasmic connections in the endosperm cells of *Diospyros* species studied is not at all similar. In *D. discolor* and *D. Ahernii* they are very numerous, and are found perforating the unpitted cell walls throughout; in *D. kaki* and *D. ebenaster* they are few, restricted, and grouped at the walls. They occur singly, or in groups of two, three, four, five, or six, and are thicker when single and usually thinner in groups.

The writer is indebted to Professor CHARLES J. CHAMBERLAIN for suggestions and advice.

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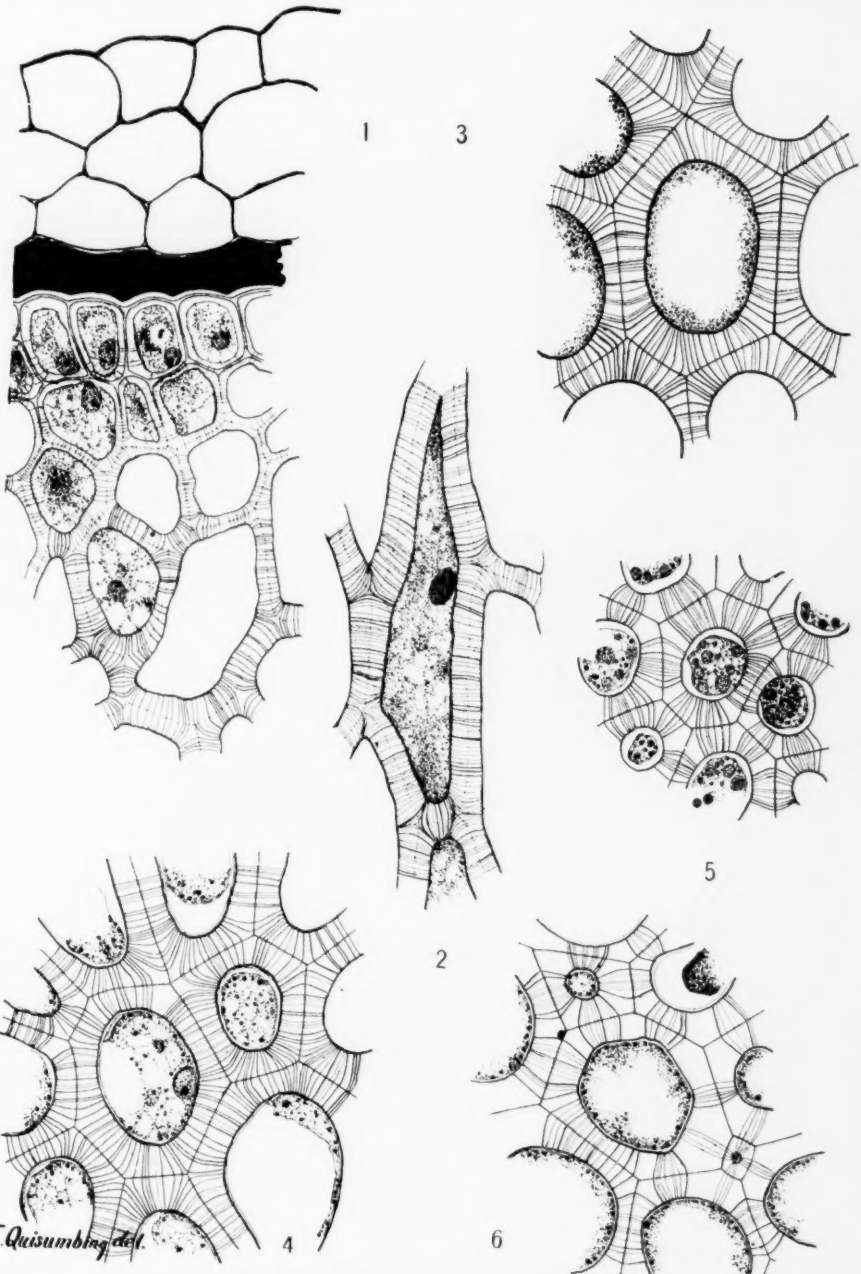
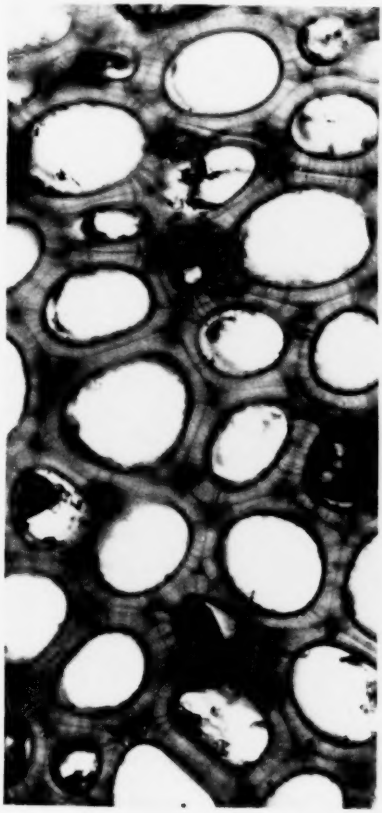


QUISUMBING on DIOSPYROS



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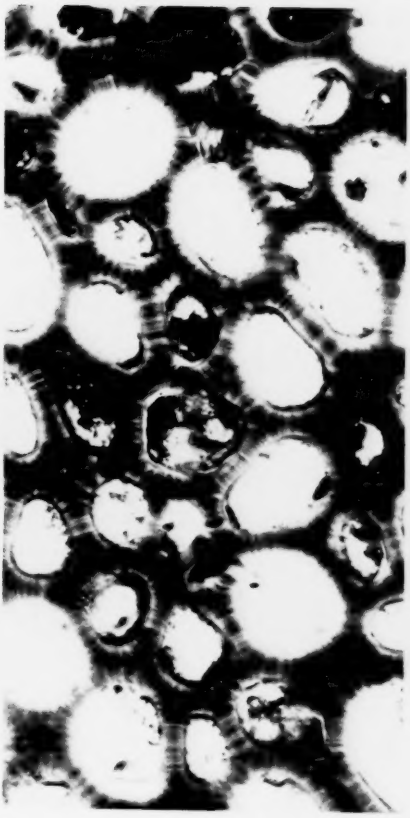

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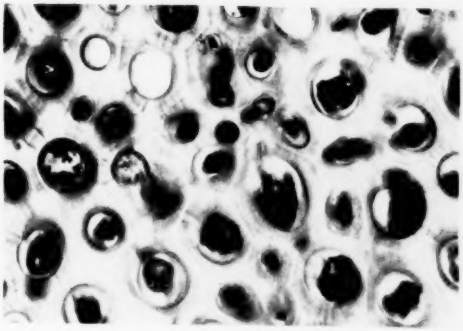

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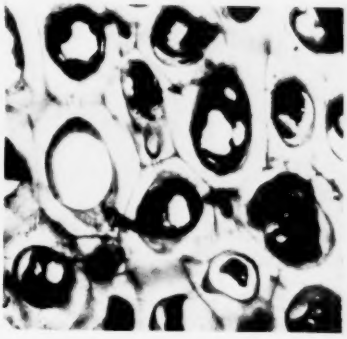

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EXPLANATION OF PLATES XXIII, XXIV

PLATE XXIII

All figures drawn with aid of Bausch and Lomb camera lucida, using Spencer 1.8 mm. N.A. 1.25 oil immersion objective and 6× eye-piece. All figures show a magnification of about 620 diameters.

FIG. 1.—*D. discolor:* portion of transverse section of ripe seed, showing few layers of testa, and outermost layers of cells of endosperm; protoplasmic connections thinnest and fewer in number at epidermal cells and layer adjacent to epidermis; nucleus and inclusions very conspicuous; walls thicker in underlying cells. This shows also apparent decrease and absence of protoplasmic connections in walls of epidermis.

FIG. 2.—*D. discolor:* elongated longitudinal cell in underlying region, at seventh layer within epidermis (note nature and number of protoplasmic connections).

FIG. 3.—*D. discolor:* portion of radial longitudinal section of ripe seed, showing nature of lumen, inclusions, thickness of walls, and protoplasmic connections.

FIG. 4.—*D. Ahernii:* portion of radial longitudinal section of ripe seed, showing numerous protoplasmic connections traversing whole wall; similar to *D. discolor*.

FIG. 5.—*D. ebenaster:* portion of radial longitudinal section of ripe seed, showing reduced number and nature of protoplasmic connections, and characteristic inclusions of cells.

FIG. 6.—*D. kaki:* portion of radial longitudinal section of ripe seed, showing nature of protoplasmic connections and inclusions of cells, which have undergone degeneration.

PLATE XXIV

All figures photomicrographed by the Bureau of Science, Manila, using C Zeiss DD 4 mm. objective, N.A. 10 and compensating ocular no. 4. All figures show a magnification of about 320 diameters.

All the photomicrographs are from radial longitudinal sections of ripe endosperm cells showing protoplasmic connections.

FIG. 7.—*D. discolor.*

FIG. 8.—*D. Ahernii.*

FIG. 9.—*D. ebenaster.*

FIG. 10.—*D. kaki.*

NOTICE

Although the residence of the editor is changed from Chicago to Yonkers, N.Y., for the coming year, he will still have charge of this journal.

All communications and manuscripts should be addressed to **Editorial Office, Room 11A, Botany Building, University of Chicago.**—J. M. C.

CURRENT LITERATURE

NOTES FOR STUDENTS

Origin of coal.—A number of important publications have appeared during the last twelve months dealing with the origin of coal. The earlier writers on this subject were BERTRAND, POTONIÉ, WHITE, JEFFREY, and THIESSEN. The new publications consist partly of continuations of the work of some of these investigators, and also some new contributions. The most conspicuous new contributions have been made by JEFFREY.[1] The memoir summarizes JEFFREY'S life work on the origin of coal in obtaining the following conclusions. He believes that coals are the results of allochthonous sedimentation in open water. It follows that he rejects any theory according to which coals are derived from autochthonous or *in situ* deposition. JEFFREY also rejects the sapropelic hypothesis of the origin of coal, and thinks that the so-called sapropelic coals are not the consequence of the extreme disintegration of vegetable materials under water, but are derived from fine materials deposited under tranquil conditions of sedimentation in open water. According to JEFFREY, algae are not an important constituent either of existing open water deposits or of so-called sapropelic coals, such as oil shales and cannels, and the bodies interpreted as algae in cannels and oil shales are believed to be entirely spores of vascular cryptogams, etc. He considers the bituminous coals to be the result of aquatic transport and deposition, and thinks that anthracites present only a further stage of devolatilization in bituminous coals. He thinks that coking coals are predominantly of woody origin, and that in large measure their quality depends upon the proportion of wood present.

JEFFREY'S book, which appeared a few months after the publication of the memoir, devotes several chapters to the origin of coal. His discussions are intended for a wider audience, and are therefore of a more popular character. A great many illustrations make the reading very easy, and the style of the book adds to the attractiveness of the study. The following coals are examined, with regard to their origin: cannel, bituminous, transitional, coking, anthracite,

[1] JEFFREY, E. C., The origin and organization of coal. Mem. Amer. Acad. Arts & Sciences **15**: 1–52. *pls. 13.* 1924.

———, Coal and civilization. pp. ix+178. *pl. 1. figs. 44.* New York: Macmillan Co. 1925.

and brown. Cannel coals were laid down, like oil rock, in tranquil water, and consisted to a predominating degree of spores, but associated with these is a large amount of grosser vegetable material. Bituminous coal is largely derived from the vegetative parts of plants, such as leaves, stems, roots, etc., as shown by the contents of coal balls. JEFFREY characterizes as transitional coals those which are in transit from one category to another, and which show portions similar to cannel, bituminous, and anthracite in consecutive lines. An interesting statement is made about the coking coals, which show large quantities of burned woods throughout their substance. JEFFREY thinks that the only reasonable explanation of these isolated fragments throughout the coking coals is that the deposits have been transported and not formed *in situ*. He assumes that anthracite, like the mass of other coals, on the evidence of structure has not been derived from materials originally accumulated under open water, nor in peat bogs. He explains the extremely high percentage of carbon by the heating and pressure which had been brought to bear upon the deposit through the slow convolutions of mountain making. Brown coals he classifies as those which grade almost imperceptibly into peat on the one hand and bituminous on the other. They are constituted mostly of pollen grains and wood. He restricts lignite to those brown coals which are composed wholly, or at least mainly, of modified wood.

Another authority who has written previously on the origin of coal has contributed two important papers during the last year.[2] In the first paper THIESSEN explains the origin of coal as primarily due to deposition *in situ* and especially in peat bogs, which is exactly the opposite of JEFFREY's claim. This is especially true of the bituminous coal, while the cannel coals are almost entirely of spore matter. He does not believe that pressure was of great effect in the carbonization of vegetable matter, and especially in the formation of anthracite by high temperatures, although he admits that pressure may have caused a greater compactness of anthracite and other coals of high specific gravity.

In his paper on the origin of bog head coals, he tries to show that these coals are not derived from spores, but from alga-like forms not heretofore known, and he mentions a living organism found in the salt lakes of South Australia, called *Elaeophyton*. These organisms produce a great amount of oil. They apparently do not decay easily, but are blown to the shore, where they form a rubber-like mass which is called coorongite. This mass burns with a bright hot flame and melts before burning. Distilled it yields about 70 per cent of oils. THIESSEN calls coorongite the peat stage of bog head coals.

The conclusions of JEFFREY and THIESSEN are radically opposite. JEFFREY rejects the *in situ* theory, and THIESSEN believes that coal was formed in peat

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[2] THIESSEN, R., The origin and constitution of coal. pp. 44. *pls. II.* Wyoming Hist. and Geol. Soc. Wilkes-Barre, Pa. 1924.

———, Origin of the bog head coals. U.S. Geol. Survey, Professional paper 132–121–138. Washington. 1925.

bogs. JEFFREY does not believe in the algal origin of certain coals, and THIESSEN thinks that a great deal of our coal originated that way. Both men represent very high standards of scientific investigation and technical ability. It will be interesting to observe whose opinions will prevail in the course of time.—A. C. NOÉ.

Temperature during flower-formation.—BLAAUW[3] has studied the effects of temperature during the period of flower formation on the development of leaves, roots, and flower clusters, and on the weight of the bulbs of the hyacinth. Eleven temperatures were used, ranging from 1.5° to 35° C. The temperatures were secured by means of thermostats placed in rooms which approximated the temperature desired. Humidity was also controlled by placing in the thermostats porous evaporation tubes. In regard to the development of the leaves, flowers, and flower clusters, it was found that at first the optimum was 23°–28°, but that during the treatment this changed, so that later on the greatest development was at the lower temperature, 17°–20°. If the development after planting was included in the observations, however, the higher temperatures were as favorable as the lower or even more so. This shifting of the optimum temperature from a higher to a lower degree is explained on the basis of cell division and cell extension requiring different optimum temperatures, a higher temperature being more favorable for cell division, and a lower for cell extension. Although after planting the bulbs kept continually at a higher temperature equaled or exceeded in development those kept continually at a lower temperature, a treatment which involved keeping the bulbs for a time at a higher temperature and then transferring them to a lower gave the most favorable results. In the case of the higher temperatures, a second high optimum was observed at 35°. Some statements as to the practical application of the researches are made. As an optimal treatment, where both flowers and leaves are desired, a treatment for eight weeks at 25°–27° and then four weeks at 17° is recommended; but when the flowers are not important, a treatment of 35° for five weeks and then 17° until planting time is recommended.

One is impressed with the amount of work that must have been required to make the numerous measurements and observations, and in keeping the constant temperatures for long periods of time. The illustrations are excellent. It would be interesting to determine what internal chemical changes are correlated with the growth responses noted.—S. V. EATON.

Survival of plants through the Ice Age.—It has generally been held by botanists and geologists that the species of plants now occupying arctic and cold temperate areas migrated southward in advance of the Pleistocene glaciers,

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[3] BLAAUW, A. H., The results of the temperature during flower-formation for the whole hyacinth. I. Koninkliijke Akad. van Wetenschappen te Amsterdam. **23**[T]: 1–66. 1924.

and later migrated northward to their present areas. FERNALD[4] now presents some very strong arguments in favor of the view that, in some instances at least, the persistence of plant species through the Ice Age was possible and even probable in areas free from glaciation. In a few places in eastern America, notably in the Gaspé Peninsula of Quebec and on the Long Range of western Newfoundland, there is an extraordinary collection of species of western America, known nowhere else east of the Rocky Mountains. These mingle with ordinary arctic-alpine species of widespread distribution. Along with these remarkable disjuncts, previously described by FERNALD, are 80 pronounced endemic species with Cordilleran affinities. The striking endemism and disjunct distribution on the Gaspé Peninsula are in sharp contrast with the lack of endemics and western disjuncts in Nova Scotia and eastern Newfoundland, where there are many species of the coastal plain, separated from the main range of these species by coastal subsidence. This splitting off of the Nova Scotia and Newfoundland coastal plain plants from their congeners to the south may have taken place 25,000 years ago, but this has not been long enough to produce any endemism to speak of. FERNALD thinks, therefore, that the endemisms of the Gaspé flora necessitate the assumption that this flora has existed there for a vastly long period of time; in other words, through the Pleistocene. It is certainly significant that these endemics and also the western disjuncts are confined to areas now recognized by the geologists to have escaped glaciation. Adjoining glaciated areas that are similar lithologically are without these species, in spite of the thousands of years since the recession of the ice. Also in favor of FERNALD'S view is the fact that Greenland, which is now subject to the rigors of continental glaciation, nevertheless has 416 species of vascular plants; more than half of these species are still found near sea level south of the St. Lawrence, and seventy-five of these species are typical plants of temperate eastern America, thus showing that even the plants of temperate climates may grow close to a continental ice sheet. The considerations so well assembled in this paper make one wonder whether the plants now residing in temperate America had to migrate so far south to escape glacial rigors as we have commonly supposed.—H. C. COWLES.

Chemical composition of sweet corn.—In picking sweet corn for the table or for canning, of course it should be picked when its chemical composition is such that it is the most palatable. In experimental work also, it may be necessary to pick ears of the same stage of ripeness. The nail test has frequently been used to predict the chemical composition of sweet corn. In applying this test, the thumb-nail is forced into the kernel, and if the exudate is milky, the corn is considered to be in the milk stage. This is the best edible stage. APPLEMAN[5] has

[4] FERNALD, M. L., Persistence of plants in unglaciated areas of boreal America. Mem. Amer. Acad. Arts & Sciences **15**: 241–342. 1925.

[5] APPLEMAN, C. O., Reliability of the nail test for predicting the chemical composition of green sweet corn. Jour. Agric. Res. **21**: 817–820. 1921.

tried to determine how closely the chemical composition of sweet corn can be predicted by the nail test. The test was applied at different stages of ripening and at the same time samples were taken for analysis. Two crops were thus tested, one ripening in August, the other in the cool autumn. It was found that the reliability of the nail test was very much affected by the rate of ripening and by the rate of water loss by evaporation. In the case of the late crop, the ripening processes took place more slowly, and less water was lost during the ripening than in the case of the early crop. Consequently, there was less variance in the chemical composition of the kernels of each stage of ripening of the late crop, than in the corresponding stage of the early crop. The nail test becomes then a fairly reliable means of predicting the chemical composition of sweet corn, especially when applied in the case of sweetcorn ripening slowly in the autumn. —S. V. EATON.

Root pressure exudates.—An account of the constituents of vine sap is given by PRIESTLEY and WORMALL,[6] the data having been published previously by WORMALL.[7] Over 90 liters of exudate were analyzed after collection under sterile conditions. The solid matter constituted 1.56 gm. per liter, of which the inorganic salts formed 0.56 gm. and the organic solids 1.00 gm. Among the organic substances found, reducing sugars were most abundant, glucose 0.29 gm. per liter, and fructose 0.04 gm. per liter. Only a small quantity of non-reducing sugar was found (0.008 gm. per liter of sucrose). Four dibasic organic acids were isolated, oxalic, succinic, tartaric, and malic. Traces of another unidentified acid were found. A very small amount of organic nitrogen occurred in the sap, the smallness of which served as an excuse to mention improbable growth hormones and accessory vitamines. The presence of several enzymes, diastase, peroxidase, and catalase, accounts more satisfactorily for the presence of this constituent.—C. A. SHULL.

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[6] PRIESTLEY, J. H., and WORMALL, A., Solutes exuded by root pressure from vines. New Phytol. **24**:24–38. 1925.

[7] WORMALL, A., The constituents of the sap of the vine (*Vitis vinifera* L.). Biochem. Jour. **18**:1187–1202. 1924.

GENERAL INDEX

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